

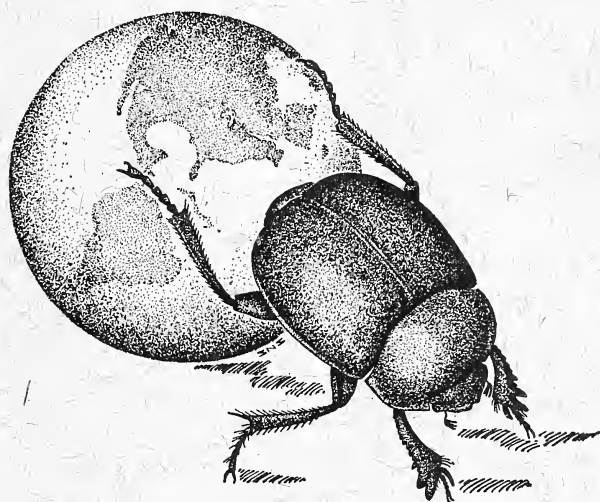
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MARCH 1980

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THE SEASONAL OCCURRENCE OF SEXUAL BROOD AND THE
PRE- AND POST-NUPTIAL BEHAVIOR OF THE HONEY ANT,
MYRMECOCYSTUS MEXICANUS WESMAEL, IN COLORADO

Dr. John R. Conway

Abstract.—Nocturnal observations and excavations of honey ant colonies in the vicinity of Colorado Springs, Colorado provided information on pre- and post-nuptial behavior and the seasonal appearance of the reproductive brood. The mating flights of three different nests were observed on the evenings of July 24, 25 and 28. The nuptial activity at one formicary lasted an hour and a half and peaked between 7:26 and 7:36 PM when the sexuals took wing. During this period 56 queens and 100–110 males were counted. Dealtated queens were observed after the nuptial flights. Queen larvae were uncovered in nests between October and February and queen cocoons were unearthed in May and June. Winged queens and males were taken from nests approximately one month prior to swarming and were noted outside colony entrances several days before and after the nuptial flights. A single wingless queen was recovered from each of the three completely excavated colonies.

Introduction

All ants are social insects, and most colonies contain three castes: queens, males and workers. Typically, males and queens are produced in numbers at certain seasons and emerge during a spectacular nuptial flight. After being inseminated, the queen sheds her wings, excavates a small burrow and nourishes the brood from her metabolized fat bodies and alary muscles (Wilson, 1974).

This paper sheds some light on the seasonal appearance and duration of the reproductive brood and the pre- and post-nuptial behavior of the honey ant, *Myrmecocystus mexicanus* Wesmael in Colorado.

Materials and Methods

Information on the presence of *M. mexicanus* reproductives was collected during the complete excavation of three formicaries and the partial unearthing of five others in the vicinity of Colorado Springs, Colorado in all months except March, April, August and November. Workers and brood from a December excavation were transferred to a vertical ant farm to study the development of reproductives under laboratory conditions.

The nuptial flights of three separate colonies were observed on the eve-

nings of July 24, July 25, and July 28. Dealated queens were located after some mating flights by searching ridge and mesa tops near the active nests with the aid of a double-mantle Coleman lantern.

Results and Discussion

Seasonal occurrence of sexual brood.—Queen larvae: Queen larvae were uncovered in formicaries at depths ranging from 36 to 144 cm. The largest number uncovered in one nest was 80 and they were found between 88 and 144 cm during the period from January 13 to February 3. The largest number, 38, was in a chamber 119 cm deep. They were probably deep in the nest to protect them from the cold temperatures characteristic of that time of the year.

Development of queen larvae begins as early as October 8 since a few were unearthed in another colony at that time. They were at depths ranging from 36 to 114 cm. From the foregoing, it is evident that the development of queens begins at least 9.7 months prior to the nuptial flight in late July. The queen larval stage is fairly long, extending from October 8 to February 3, a period of approximately 4 months.

Queen pupae: Queen pupae were uncovered in two colonies at depths ranging from 6 to 178 cm during the period from May 31 to June 22. As a result they were both closer to the surface and deeper in the nests than the queen larvae.

Over 176 queen cocoons were removed from one nest in June, suggesting the tremendous reproductive potential of a single colony. This figure is over twice the maximum number of queen larvae uncovered in January and February and leads to speculation that the number of queen larvae does not peak until sometime between February and June.

The pupal stage appears to be considerably shorter than the larval stage. Queen pupae were uncovered in formicaries between May 31 and June 22, a period only 23 days long, and only 1.8 months prior to swarming. Queen pupae appeared in the laboratory vertical nest much earlier, on January 14, but their development was probably speeded by the warmer indoor temperatures.

Queen cocoons were not observed during excavations between late July and February. Apparently adults hatch in June and the pupae do not reappear until the following spring.

Males and winged queens: Both males and alate queens were unearthed in a colony as early as June 22, about a month before swarming, in chambers at 36 cm, 48 cm, and 50 cm, but only males were present in two deeper chambers at 64 cm and 83 cm. Winged queens were also taken from sub-surface passages. Males and an alate queen were found below a rock at the surface at another nest on July 16. This suggests that males and queens are

at first deep in the nest, with males being deepest, but that they approach the surface as the time of the nuptial flight approaches.

Others have reported adult reproductives present in the nests even earlier. Gregg (1963) recorded males and females of *M. mexicanus* in colonies on June 2 and Snelling (1976) noted reproductives of *Myrmecocystus* in nests up to three months prior to their mating flight. Cazier and Mortenson (1965) reported winged males and females of *M. mimicus* in subsurface burrows, 3 to 8 cm deep, as early as March 9, even though their nuptial flights occur in late July and early August. This is a holding period of more than five months.

Two newly-hatched winged queens appeared in my vertical laboratory colony on February 28, approximately five months in advance of the nuptial flight. But surprisingly, the first male did not appear in this nest until July 14, just two weeks prior to when the nuptial flight would ordinarily occur. These unusual developmental times are attributed to the unnatural laboratory conditions.

Wingless queen: A single wingless queen was taken from each of the three completely excavated nests. At one formicary she was in the second deepest chamber at 138 cm along with 40 repletes, 3 depleted repletes, 2 semi-repletes, 25 queen larvae, many small larvae, and 1,819 workers. The queen of another colony was in the 8 cm by 16 cm bottom chamber at a depth of 178 cm, which also contained 2 flaccid repletes, 8 semi-repletes, 13 depleted repletes, 2 queen cocoons, many small larvae, about 700 workers, and the remains of a wasp.

An exception was the third nest, where the queen was taken from a chamber only 14 cm deep along with many small larvae and many workers. She was in poor condition and could only move her legs and antennae slightly, possibly due to injuries sustained when workers dragged her through the passages to escape excavation.

McCook (1882), Creighton and Crandall (1954) and Snelling (1976) also report but a single gravid female per colony. Thus, there appears to be but one wingless queen, who is usually in the lowest part of the nest accompanied by repletes (in various stages of distension), brood, and a large contingent of workers.

Appearance of reproductives before and after the nuptial flight.—Reproductives appeared outside the entrances of the Colorado Springs nests several days prior to swarming. This probably is a result of the fact that sexuals display a circadian rhythm, with sharp increases in restlessness, at just the hour each day at which the nuptial flights occur (McCluskey, 1967).

Males were observed outside the entrances as early as July 14, 10 to 14 days prior to swarming, and interacted with the workers. For example, on one occasion a male left the entrance despite the efforts of a worker trying to pull him back in. Another time a male went off the crater and a major

scurried about the cone as if searching for him. Males were even observed being carried back to the nest by workers. But, on another occasion, it was a worker who carried the male out of the entrance prematurely.

Winged queens were observed outside the entrances as early as July 20, four to eight days before the nuptial flights. Some queens left the crater and wandered away, while others went out and then returned. A dead winged queen was found near the entrance of one nest four days before the nuptial flight. Snelling (1976) reported a *M. mexicanus* queen outside a nest as early as June 27.

At some nests winged queens and males were observed several days after the nuptial flight. In fact, the last sighting of males and alate queens was on July 29, one to five days after the observed nuptial flights. Snelling (1976) reported *M. mexicanus* queens still in the nests as late as September 29.

Pre-nuptial activity.—The nuptial flights and pre-nuptial behavior of three different colonies in the Colorado Springs region were observed on July 24, July 25 and July 28. Slocumb (1966) reported mating flights at seven colonies on the plains east of Colorado Springs as late as August 2. On the other hand, Paul Nesbit, a local naturalist, noted a nuptial flight in the Garden of the Gods on July 19, and recalled honey ants swarming as early as July 3 (personal communication). Thus, while this activity may occur anytime during a one month period, it usually takes place in the last half of July.

Snelling (1976) reports that flights of *M. mexicanus* in eastern Arizona, New Mexico and Colorado occur during the summer months, usually following an afternoon rain, and that in southern California, because of the dry summers, these flights are postponed until the first fall rains.

There was some correlation with precipitation in the Colorado colonies. It rained the night before swarming at two nests and at a third colony, it rained both the day before and the afternoon preceding the flight.

Pre-nuptial activity began somewhat earlier in the evening than the usual nocturnal exodus which commenced at 7:30 PM (Mountain Standard Time), on the average. For example, on July 28, there were already 5 queens and 6 males in the entrance and surrounded by workers at one Colorado Springs nest when observation began at 7:00 PM. Four queens and 21 males appeared at 7:10 PM when the air temperature was 21°C. Males lined the entrance, surrounded by workers on the crater, while queens periodically came up and then receded from view. As more queens and males emerged, they almost completely filled the entrance. Eight queens and 32 males ventured farther from the opening at 7:19 PM. By 7:23 PM there were 24 queens and 40 males advancing onto the crater and a number reached the outer edge a minute later. The overall worker activity increased greatly at 7:26 PM, when 42 queens and about 100–110 males were counted. Field observations on *M. mimicus* also indicated worker excitement around the nest entrance just prior to and during emergence of the winged sexuals (Cazier

and Mortenson, 1965). By 7:27 PM, reproductives were going off the crater in all directions. Fifty-four queens and an estimated 70 males had advanced about 0.6 m from the entrance at 7:29 PM. First a male took wing and rose straight up, and then a few queens attempted to fly. Snelling (1976) reports that males generally precede the females by several minutes. At 7:33 PM a queen finally lifted off successfully. Some queens scaled grass tussocks, but most tried to take off from the ground, usually after buzzing about the surface futilely for a time. They then soared straight up and out of sight. Queens took wing in all directions at 7:36 PM, but the flights were difficult to follow due to impending darkness. Workers nipped at the queens on the ground, apparently to prevent them from returning to the crater and to induce them to fly. Thirty queens and 80 to 90 males were present at 7:42 PM. Nine queens and several males were seen around the crater at 7:50 PM as the nuptial activity waned. At 8:04 PM there was but one queen and a reduced number of workers on the crater. By 8:21 PM there was little activity, and the number of ants on the crater was greatly diminished. A few workers were seen a short distance from the entrance, and one was carrying a dead insect. Cazier and Mortenson (1965) also reported workers foraging during the nuptial activities. The last queen peered out the entrance at 8:21 PM, and then withdrew. As mentioned previously, unsuccessful winged queens and males were observed several days after the nuptial flight, but their ultimate fate in the colony is unknown.

The swarming of this nest lasted an hour and a half and peaked between 7:26 and 7:36 PM. Altogether 56 queens were collected (many escaped) and 100 to 110 males were counted during the pre-nuptial activity. Nesbit (personal communication) observed a nuptial flight of *M. mexicanus* in the Garden of the Gods, during which he counted only half as many queens (28) but approximately the same number of males (100).

Another colony was somewhat atypical in that flight attempts were observed on three nights, July 22, 23, and 24, instead of on only one night. This may have resulted from rain at the time of the nuptial flight on those evenings. In any event, the queens actually took off only on July 24. Another peculiarity of this nest was that the queens made a mass exodus twice on July 23, once at 7:10 PM and later at 7:30 PM, but returned after each departure.

In summary, queens and males first left the three observed colonies between 7:10 and 7:30 PM. Slocumb (1966) saw them exit from plains nests even later, at 7:40 PM. Reproductives attempted to fly or took wing at times ranging from 7:22 to 7:36 PM. Swarming ended when the unsuccessful queens and males returned to the formicary, and this occurred between 7:40 and 8:04 PM. Slocumb (1966) reported that they came back later, at 8:30 PM.

Wingless queens: Although mating was not observed, it is presumed to

occur during the crepuscular nuptial flight. It is possible that multiple inseminations take place since they have been observed in a number of formicine species (Wilson, 1974).

Pre-nuptial activity was observed at a colony on a mesa dotted with similar nests on July 25, and a total of eight dealated queens were collected later that evening. The first one was found at 8:05 PM on a nearby side ridge, about a half hour after the nuptial flight. The others were captured about 0.6 km away on the eastern end of the mesa, between 8:58 and 11:38 PM.

There is evidence that queens may not dig burrows until the night after the nuptial flight. For example, on July 26, another dealated queen was observed starting to dig a burrow at 6:20 PM, an hour before the normal nuptial flight for that evening.

On July 27, at 8:50 PM, two more wingless queens were discovered digging burrows in the same region. Interestingly, one was digging in a clearing around a *Pogonomyrmex occidentalis* colony. Mature *M. mexicanus* nests have been observed in the immediate vicinity of this species on four other occasions. Apparently they can tolerate the close proximity and avoid competition by being active at different times during the day and night. The last queen to excavate a burrow in this area was found on August 4, ten days after swarming was first observed.

The queen-burrow entrances, which are 5 mm in diameter, were eventually closed with a plug of earth. The first closed entrance was noted on July 27, two days after the nuptial flight. Snelling (1976) reports that *Myrmecocystus* queens dig to a depth of 15 and 46 cm before constructing a brood chamber.

Four queen-burrows on the mesa were marked with rock cairns and left for future observation. All four were closed by July 29, four days after swarming, but unfortunately none reopened the following summer. This may be indicative of the high mortality generally reported for colonizing queens.

Another wingless queen was collected the following summer on July 23 in the same area. Thus, dealated queens of *M. mexicanus* were found between July 23 and August 4, but no males were observed after the nuptial flights.

Conclusions

Swarming in *M. mexicanus* in the Colorado Springs area typically occurs about dusk on one evening in late July and may be associated with precipitation up to a day in advance. Specifically, it was observed at three different colonies on July 24, 25 and 28.

Pre-nuptial activity begins somewhat earlier in the evening than the usual stirrings, but interestingly, the peak activity, when the queens and males

took wing, occurred at approximately the same time, 7:30 PM, as the normal foraging exodus. In fact, after the flight the colony resumes its search for food.

At one nest the pre- and post-nuptial activity lasted about an hour and a half, during which time 56 queens were collected and 100 to 110 drones were counted. Swarming ended when the unsuccessful queens and males returned to the formicaries, and this occurred between 7:40 and 8:04 PM.

Although honey ants are reasonably abundant in the Colorado Springs area there are several flaws in the nuptial process which probably restrict their numbers:

1. Not all queens and males participate in the nuptial flight, since some return to the colony afterwards.
2. Adverse weather may desynchronize the process and interfere with aerial union. At one nest queens and males exited on three successive nights but took wing on only one evening.
3. A few males and females leave nest entrances several days prior to the flights and some are undoubtedly lost.
4. There appears to be a high mortality among the founding queens which greatly decreases the reproductive potential.
5. The queens and colonies have rather specific habitat preferences, generally being found on the tops of ridges or mesas between 5,000 and 7,000 feet.

The metamorphosis of queens begins with the appearance of queen larvae in October, approximately ten months prior to the nuptial flight. This developmental stage appears to be the longest, persisting at least four months until February and perhaps longer.

Queen pupae were unearthed as early as May 31, about two months prior to swarming, but were actually observed in the nests for only 23 days. Thus, this stage may last less than one-fourth as long as the queen larval stage. Over 176 queen cocoons were recovered from one nest, suggesting the large numbers of queens which may be produced.

Adult males and females were removed from colonies as early as June 22, about one month prior to swarming, and a period just slightly longer than the pupal stage. This data needs to be carefully reexamined however, especially in light of reports of reproductives being present up to five months in advance of the nuptial flight.

The discovery of but a single wingless mother queen in each nest is consistent with the findings of most investigators.

Thirteen dealated queens were located after the mating flights between July 23 and August 4. No males were found after the flights. Usually the queens began to excavate their burrows within one-half to four hours after

the flight, but one appeared to have delayed until the next evening, when she was observed digging an hour in advance of the time for the flight.

The queen-burrow entrances were 5 mm in diameter, but began to be closed only two days after the flight. Four closed entrances were marked for future observation, but none reopened. These probably are indicative of a high mortality rate among founding-queens.

Acknowledgments

I am indebted to Paul Nesbit who helped me locate *M. mexicanus* colonies in the Garden of the Gods and allowed me to observe the nuptial activities of a nest in his yard. Throughout the course of this investigation, R. E. Gregg has made many valuable suggestions.

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Department of Biology, Elmhurst College, Elmhurst, Illinois 60126

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DIGESTIVE SYSTEM AND ASSOCIATED ORGANS IN THE ADULT
AND PUPAL MALE DORYLINE ANT *AENICTUS GRACILIS*
EMERY (HYMENOPTERA: FORMICIDAE)¹

S. Shyamalanath and James Forbes

Abstract.—This paper presents the first description of the anatomy and histology of the alimentary tract, the postpharyngeal glands, the salivary glands, the Malpighian tubules, and the mandibular glands in the male adult and pupa of the Old World doryline ant, *Aenictus gracilis*. The alimentary tract consists of the cibarium, the buccal tube, the infrabuccal chamber, the pharynx, the oesophagus, the cardiac valve, the ventriculus, the pylorus, the intestine, the rectal valve and the rectum. In the adult the infrabuccal chamber lies posterior to its usual position in ants under the posterior floor of the buccal tube and the anterior pharynx, while the pupa has a recess where the infrabuccal chamber is usually present. The pharynx is divisible into a broad anterior, an indented middle, and a tubular posterior region into which the postpharyngeal glands open. The epithelium of the pharynx has flattened cells in the adult and low columnar cells in the pupa. The intima of the postpharyngeal glands and ducts bears long hair-like projections. Maxillary glands are absent. The epithelium of the oesophagus has small folds in the pupa and the lumen is wider than in the adult. The continuation of the oesophagus into the ventriculus is the cardiac valve. A crop and a proventriculus are absent. The ventriculus has a dorsal concavity toward its posterior half. The ventricular epithelium of the adult consists of digestive and regenerative cells. In the pupa the ventricular epithelium has disintegrating and regenerating regions. The regenerating digestive cells are of three distinct types that represent stages in the maturity of the epithelium. The pylorus is internally divided into an anterior region where the 18–20 Malpighian tubules enter, and a posterior region. The posterior extension of the intestine into the rectum is the rectal valve. The inner wall of the rectum has 3 rectal pads. The very small salivary glands are of the simple branched acinar type, and their ducts have a tortuous cuticular lined lumen. The mandibular gland consists of about 12 pyriform cells and a reservoir. Comparisons made with the other Old World and New World species previously described have revealed features of phylogenetic importance that lend support to the concept of the triphyletic origin of the dorylines.

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The study of the morphology, anatomy and histology of male ants is of particular importance because as Janet (1902) recognized, they are the least specialized of all of the nest forms and most wasp-like in appearance. This wasp-like appearance offers evidence that ants evolved from wasp-like insects. A review of the literature on the anatomy of ants indicates that the males have been studied only in a very few of the numerous genera and species. These studies have brought to light anatomical and histological differences in the organs and systems at the subfamily, generic, and in some even at the species level, that are of phylogenetic importance. As stated by Wheeler (1910) the males are stable in structure and, if more readily obtainable, would be valuable in the taxonomy of the group.

The digestive system of male ants was first described by Meinert (1861) in a formicine, *Formica rufa*, and a myrmicine, *Myrmica ruginodis*. He illustrated differences in the structure of the proventriculus in these two species; this was the first indication of the importance of this organ as a basis for determining phylogenetic relationships of various genera of ants. Forel (1878) and Emery (1888) used the diverse features of the proventriculus for taxonomic purposes. Descriptions of the anatomy of the digestive system that followed were those of Janet (1902) in the gaster of a myrmicine, *Myrmica rubra*, Mukerjee (1926) in an Old World doryline, *Dorylus labiatus*, Marcus (1953) in a dolichoderine, *Dorymyrmex emmaericaellus*. A comprehensive and comparative study of the proventriculus in ants was made by Eisner (1957), who formulated a phylogenetic dendrogram in which he placed the dorylines parallel to the poneroid complex but with a different origin than had been postulated for other groups of ants. More recent observations of this organ are those of a ponerine, *Rhytidoponera metallica*, (Hagopian 1963), and two species of myrmicines, *Myrmica rubra*, (Trachimas 1967), and *Solenopsis invicta* (Buren 1972) = *S. saevissima richteri* Forel (Tice 1967). The present investigation has revealed the absence of a crop and a proventriculus in both the adult and pupa of the male of *Aenictus gracilis*. Prior to Eisner's paper (1957), Brown (1954) in a study on the phylogeny of ants stated that the precise affinities of the dorylines are unknown, and it is possible that they are diphyletic in origin. Gotwald (1969) in his exhaustive study of the mouthparts of 104 species of ants revealed distinct differences between the New World and Old World dorylines, and in the Old World doryline genera between *Dorylus* and *Aenictus*. Thus he advocated a triphyletic origin for the dorylines separating the tribes Dorylini, Aenictini, and Ecitonini from one another. Schneirla (1971) considered dorylines as monophyletic in origin on the basis of functional and behavioral evidence.

In addition to the above mentioned papers on the digestive system of ants, three other reports have been published on the internal anatomy of the

New World doryline workers (Whelden 1963, Gotwald 1971, Gotwald and Kupiec 1975).

The present work is the first comprehensive anatomical and histological description of the digestive system of the male adult and pupa of the Old World doryline *Aenictus gracilis*. Comparisons are made with those of the other dorylines previously described.

Materials and Methods

The 12 male adults, and the 12 pupae at an advanced stage of development used in this study were collected by the late Dr. T. C. Schneirla from a bivouac on an eastern mountain slope above Dumaguete City, Negros Island, Philippine Islands, in 1962. The specimens were preserved in 70% ethyl alcohol. Each specimen was mounted on paraffin in a Syracuse watch glass and dissected under 70% ethyl alcohol. Whole mounts of organs were prepared by Lynch's precipitated borax-carmin method (Galigher and Kozloff 1971), and specimens for histological study were processed by a double infiltration technic (Trombetta and Forbes 1977). Frontal, sagittal, and transverse serial sections were cut and stained with Harris' haematoxylin, counterstained with eosin and mounted in euparal. Drawings were made with the aid of a camera lucida and a B & L trisimplex microprojector.

Anatomy of the Digestive System

The anteriormost part of the alimentary tract in the adult and pupa is the cibarium that leads into a wide dorsoventrally compressed buccal tube. The thin-walled buccal tube is broader anteriorly, and in the adult the posterior floor opens into an elongated, flattened infrabuccal chamber that extends beneath the anterior pharynx (Fig. 1). In the pupa an irregular recess is located beneath the anterior floor of the buccal tube, where the infrabuccal chamber is normally found in ants (Fig. 2). The pharynx that continues is distinguishable into a broad anterior, an indented middle, and a tubular posterior region. The lateral margins of the anterior region become progressively more sclerotized posteriorly into the indented region. Bundles of muscle fibers extend from the dorsal surface of the anterior region to the inner, anterior surface of the head capsule. Arising from the dorsolateral wall on each side of the posterior region of the pharynx is a duct that divides into numerous branching, and convoluted tubular postpharyngeal glands. These glands extend anteriorly as far as the buccal tube and laterally and posteriorly over the front part of the brain. The posterior end of the pharynx continues as a narrow oesophagus passing between the brain dorsally and the suboesophageal ganglion ventrally and through the neck, the thorax, and the petiole into the gaster. In the gaster, about the beginning of the 4th

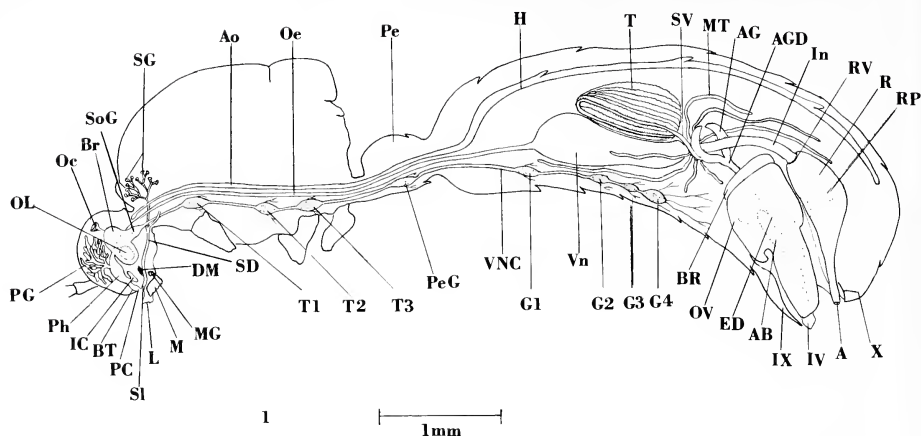
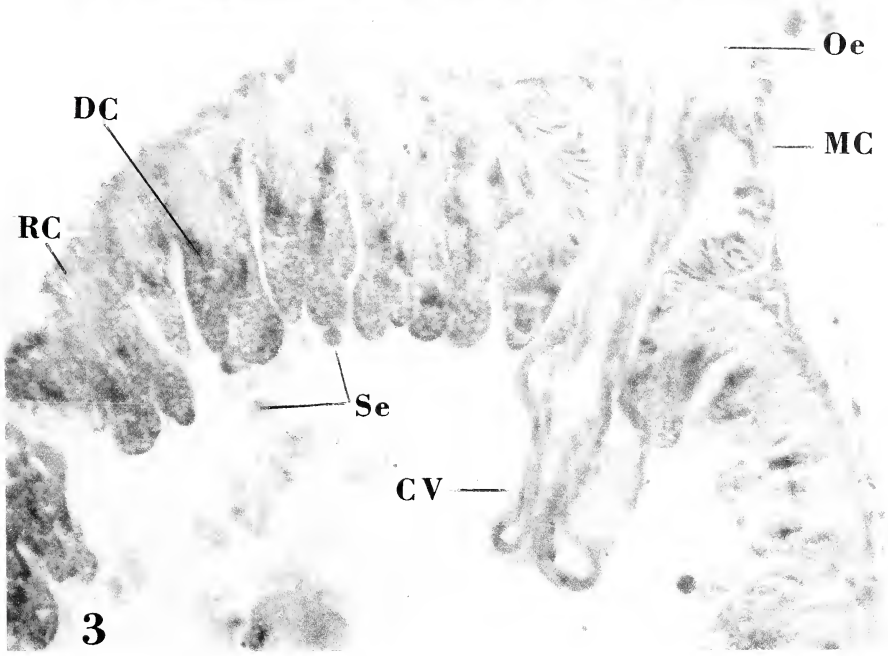
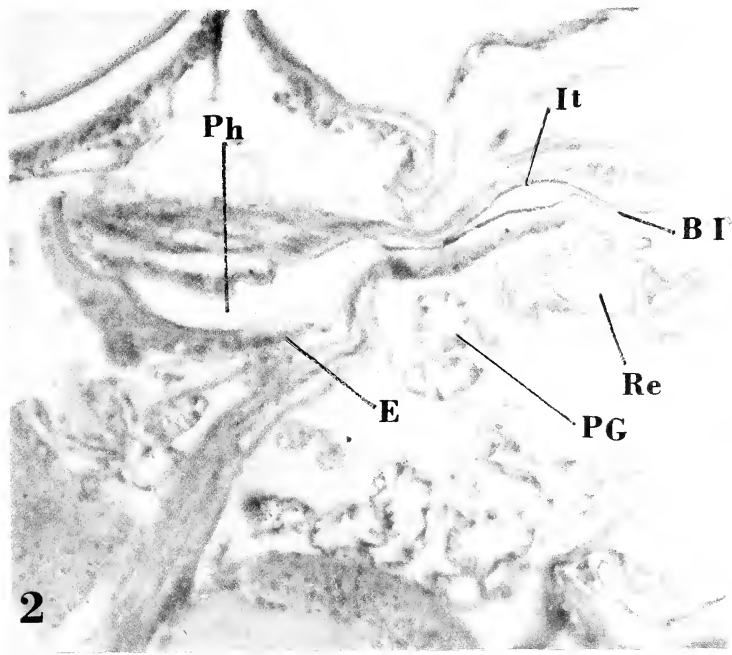


Fig. 1. Diagram of a lateral dissection of the adult male of *A. gracilis*.

ABBREVIATIONS

A, anus; AB, aedeagal bladder; AG, accessory gland; AGD, accessory gland duct; Ao, aorta; B, basal cell layer; Br, brain; BR, basal ring; BT, buccal tube; CV, cardiac valve; DC, DC1, DC2, DC3, digestive cells; DM, dilator muscle; Dt, ductule; E, epithelium; ED, ejaculatory duct; Ey, lower part of the eye; G1, G2, G3, G4, gastric ganglia; GC, glandular cell; H, heart; I, inner cell layer; IC, infrabuccal chamber; In, intestine; It, intima; IV, inner genitalic valve; L, labium; Lu, lumen; M, mandible; MC, muscle coat; MG, mandibular gland; MT, Malpighian tubule; Oc, ocellus; Oe, oesophagus; OL, optic lobe; OV, outer genitalic valve; PC, preoral cavity; Pe, petiole; PeG, petiolar ganglion; PG, postpharyngeal gland; Ph, pharynx; R, rectum; RC, regenerative cell; Re, recess; RP, rectal pad or gland; Rv, reservoir; RV, rectal valve; SD, salivary duct; Se, secretion; SG, salivary gland; SI, salivarium; SoG, suboesophageal ganglion; T, testis; T1, T2, T3, thoracic ganglia; Vn, ventriculus; VNC, ventral nerve cord; IX, 9th abdominal sternum; X, 10th abdominal tergum

abdominal segment, the oesophagus projects into the ventriculus and forms a cardiac valve. The ventriculus is the largest organ of the alimentary tract and extends to the middle of the 5th abdominal segment. Its anterior half is broadly rounded, the posterior half is narrower and has a dorsal concavity. The distal end of the ventriculus is constricted at the junction with the intestine. The proximal region of the intestine is the slightly wider pylorus where the Malpighian tubules enter. The rest of the intestine occupies the 5th through the 7th abdominal segments, and about halfway along it bends dorsally, increases slightly in diameter, projects into the rectum, and forms a rectal valve. The rectum is a thin-walled, pyriform sac in the 8th and the 9th abdominal segments and lies above the genital chamber. The inner wall of the anterior region of the rectum has 3 rectal pads; two are lateral and one is ventral in position. The rectum tapers to the anus that opens to the outside on the ventral surface of the 10th tergum.



Figs. 2-3. 2. Photomicrograph of a sagittal section of the head of the male pupa to show the buccal tube and pharynx. $\times 450$; 3. Photomicrograph of a sagittal section of the cardiac valve and anterior part of the ventriculus of the adult male. $\times 400$.

Histology of the Digestive System

The epithelium of the buccal tube and the infrabuccal chamber is composed of a single layer of small, squamous cells with very small, centrally located nuclei and is lined by an intima. The intima on the roof of the buccal tube is thinnest anteriorly, thickest, transversely ridged and weakly sclerotized in the midregion, and thinner and more sclerotized with small hair-like processes in the posterior region. The intima on the floor and in the infrabuccal chamber is very thin. The epithelium is not surrounded by a muscle coat in this region. In the pupa, the epithelium of the buccal tube is composed of cuboidal to low columnar cells. The intima throughout this region is uniformly thicker than that in the adult and has hair-like processes along the floor pointing toward the preoral cavity.

The epithelium of the pharynx is composed of a single layer of flattened cells with oval nuclei. The intima in the proximal part of the anterior region on the roof and floor is thick, sclerotized and forms plate-like layers, and sharp, hair-like processes on the floor project forward. Muscles are present only on the roof of this region and consist of the oblique fibers that extend to the head capsule and some longitudinal bundles that extend from front to back. In the distal part of this anterior region, the lateral walls are curved dorsally, and here the intima is more sclerotized than on the roof and floor. There are three bundles of longitudinal muscle fibers separated by two bundles of the oblique fibers. In addition, on the ventral side transverse muscle fibers extend between the ventrolateral margins of the pharynx. The middle indented region has heavily sclerotized, sharp, dorsal extensions of the lateral margins and the lumen is U-shaped. The muscles here consist of longitudinal and the oblique fibers in the dorsal concavity and transverse fibers that connect the dorsolateral arms. The distal region of the pharynx has an intima that is thicker along the floor. The muscles in this region are a continuation of those of the indented region. In the pupa, low columnar cells form the epithelium of the pharynx and the intima is thin and not sclerotized.

The postpharyngeal glands have a single-layered cuboidal epithelium. The cytoplasm is acidophilic, granular, and vacuolated, and the small oval nuclei are basally located. The glands and ducts are lined by a thin intima bearing long, hair-like projections. The lumina are devoid of any secretion. In the pupa the epithelium of these glands is folded and composed of low cuboidal or squamous cells with spherical or flattened nuclei. The hair-like projections of the intima are less numerous than in the adult, and the lumen is more spacious (Fig. 2).

The oesophagus has a low cuboidal epithelium, longitudinally folded inward to form 4 or 5 ridges, and covered by a thin intima. Toward the distal end the folds are reduced in height and the lumen is wider. The muscle coat is composed of inner longitudinal fibers, some extending into the epithelial

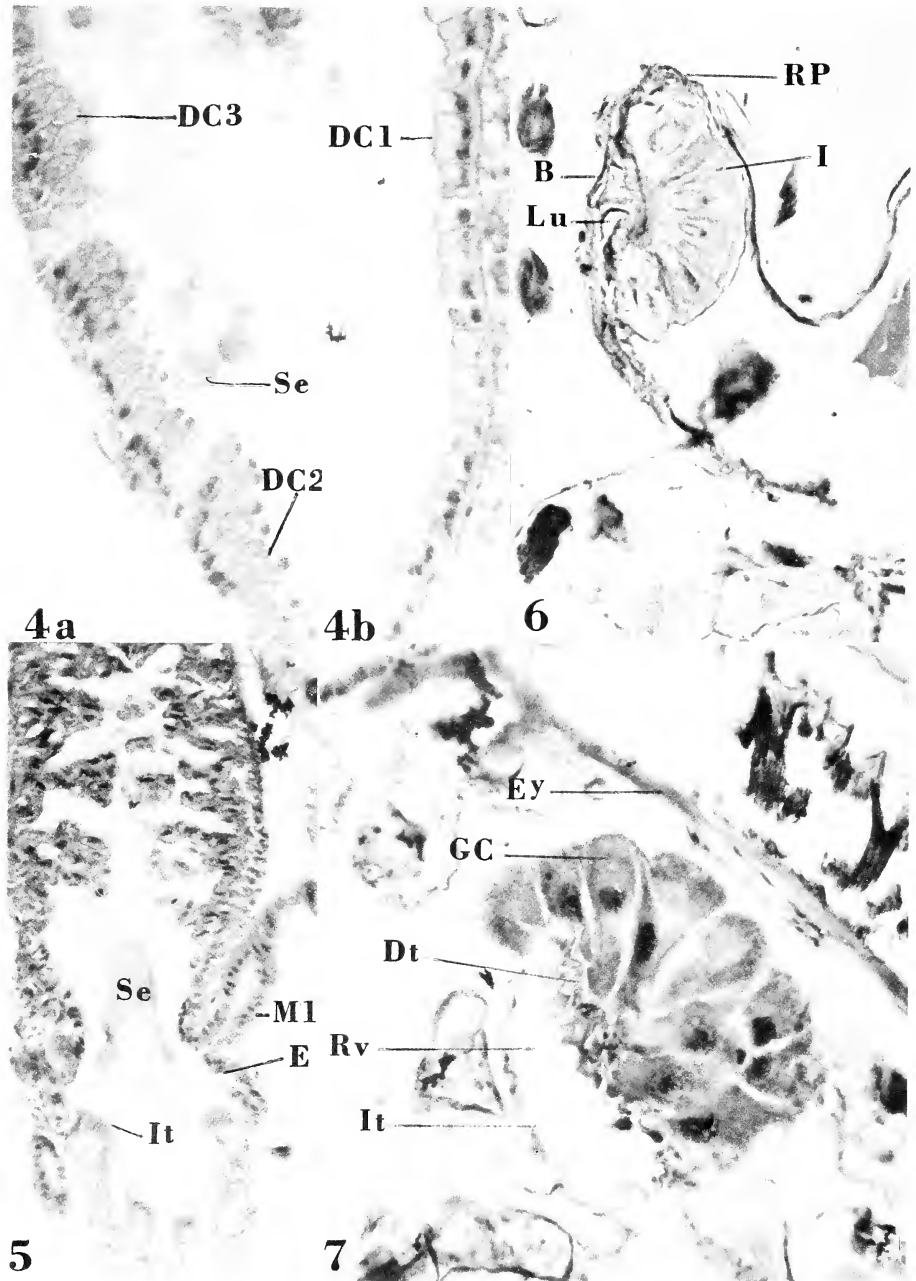
folds, and outer circular fibers. Toward the distal end a layer of 1 or 2 longitudinal fibers is present around the circular layer. In the pupa epithelial folds are small and the lumen is wider.

In the adult and pupa the cardiac or stomodaeal valve has a reflected, low cuboidal epithelium (Fig. 3). The intima terminates at the base of the outer walls of the valve. No muscle fibers are present within the valve.

The epithelium of the ventriculus is composed of large columnar, digestive or secretory cells, and small pyramidal, regenerative cells (Fig. 3). Some of the digestive cells are tall and narrow and their free ends are swollen and globular. In many of these cells the nucleus has migrated upward to the globular region and is compact and irregular in shape. The cytoplasm is neutral in its staining reaction and has basophilic granules throughout. In some of these cells granules are concentrated toward the free margin. The globular ends of some have ruptured and discharged the granular material into the lumen of the ventriculus. The regenerative cells are widely scattered clusters of a few cells each. They have a basophilic cytoplasm and oval nuclei. The muscle coat surrounding the epithelium consists of an inner circular and an outer longitudinal layer that are about equal in thickness; the fibers of the outer layer are widely separated. Sections of the pupal ventriculus show that the epithelium of the mid and posterior regions is disintegrating, while that of the anterior and some of the midregions is regenerating (Figs. 4a and b). The disintegrating cells are columnar in shape, and their basally located nuclei are irregular in shape. The cytoplasm is filled with fine, basophilic granules and small vacuoles. The free surfaces of the cells are broken and the cytoplasmic material is released into the lumen. The regenerating cells in the anterior ventral region are low, broad cells with basally located, compact, spherical nuclei. The cytoplasm is finely granular and homogeneous throughout with a thin compact layer of granules just underneath the free surface. On the anterior dorsal region the cells are tall, narrow columnar cells and the free surface is swollen and contains an acidophilic secretion. In the midregion these cells on the ventral side are also short and broad while those on the dorsal side are tall and narrow. The cytoplasm of these cells in this region is uniformly granular, and the nuclei are basally located and ellipsoidal in shape.

In the adult and pupa the pylorus is divided into anterior and posterior portions by an inward fold of the epithelium (Fig. 5). Low columnar cells in the anterior region, taller and wider cells over the fold, and small cuboidal cells in the posterior region form the epithelium. The cytoplasm is compact, finely granular and acidophilic. The intima, seen in some sections just behind the entrance of the Malpighian tubules, is always more distinct over the epithelial fold. Inner circular and outer longitudinal fibers form the muscle coat.

The intestine in the adult and pupa has a folded, cuboidal epithelium



Figs. 4-7. 4. Photomicrographs of sagittal sections of the ventriculus of the male pupa. $\times 325$. a. Dorsal wall and b. Ventral wall; 5. Photomicrograph of a sagittal section of the ventriculus and pylorus of the adult male. $\times 215$; 6. Photomicrograph of an oblique section of the rectum of the adult male to show a rectal pad. $\times 225$; 7. Photomicrograph of a sagittal section of the head of the adult male to show the mandibular gland. $\times 300$.

covered by a distinct intima. The cells of the folds are taller, but the folds diminish in height and disappear toward the distal region. The lumen contains a finely granular basophilic secretion. An inner very thin layer of longitudinal muscle, a middle compact layer of circular muscle, and an outer layer of longitudinal fibers form the muscle coat. The epithelium and the muscle coat project into the rectum and form a rectal valve. Here, the circular muscle layer is thick and forms a sphincter.

In the adult and pupa the rectal epithelium is a single layer of flattened squamous cells covered by an intima. The nuclei are spindle-shaped. The muscles consist of a single layer of circular fibers and scattered longitudinal fibers. A heavier band of circular muscle surrounds the anus and forms the anal sphincter. Each rectal pad is composed of an inner tall, columnar layer and a basal cuboidal layer separated by a lumen (Fig. 6). The inner columnar layer of cells is a continuation of the epithelium of the rectum, and the transition from the squamous to columnar cells is abrupt. The cytoplasm of the inner and the basal cells is vacuolated and has basophilic granules. The inner cells are faintly striated toward the lumen between the cell layers. The intima covering the rectal pad is slightly thicker than that lining the rectum.

The adult and pupa have 18 to 20 long, slender Malpighian tubules that open into the anterior end of the intestine at the pylorus (Fig. 5). They lie coiled around the intestine and the accessory glands of the reproductive system, some extending anteriorly as far as the proximal region of the ventriculus and some posteriorly as far as the rectum. The epithelium is composed of a layer of 4 or 5 large cuboidal cells with a striated free surface. The large nucleus has a prominent nucleolus and chromatin material. The cytoplasm has coarse basophilic granules. The lumen is filled with a neutral, granular secretion.

The salivary glands are microscopic in size and are located in the lateral regions of the prothorax (Fig. 1). In the early stages of this work when the organs and systems of the adults and pupae were dissected and studied as whole mount preparations, the salivary glands and the gland ducts were not recognizable. The salivary duct in the head and the lateral ducts in the neck region were found. Examination of the serial sections did reveal the glands and their ducts, and the following description is based on these observations. The glands are simple branched acinar glands and the acini are clustered or distributed singly and interspersed in the fat cells. Each acinus consists of a layer of pyramidal cells around a small lumen lined by a thin intima and built on a distinct basement membrane. The cytoplasm of these cells in the adult is homogeneous and basophilic with some vacuoles, while in the pupa it is more vacuolated with large basophilic granules. The nuclei are spherical or oval and centrally or basally located. The collecting ducts, the lateral salivary ducts and the common salivary duct are composed of cuboidal cells with ellipsoidal nuclei. The lumen of the salivary ducts, lined

with a heavy intima that has annular thickenings, is tortuous and forms U-shaped loops within the cells of the ducts. The common salivary duct proceeds below the brain and opens into the salivarium which is situated between the hypopharynx and the labium. Where the salivary duct opens into the salivarium a dilator muscle extends from the roof of the duct to the ventral wall of the hypopharynx.

The adult and pupa have a pair of mandibular glands located at the bases of the mandibles (Fig. 1). Each consists of a glandular portion and a reservoir. The glandular portion is hemispherical with about 12 pyriform glandular cells with intercellular spaces between them (Fig. 7). These intercellular spaces are lined with a thin cuticle. The glandular portion is encased in a thin membrane. The cells open by small ductules into the thin-walled reservoir, and the intercellular spaces converge toward the reservoir. A short duct leading from the reservoir opens laterally at the base of the mandible. The cytoplasm of the glandular cells is homogeneous with fine basophilic granules. The spherical or oval nucleus has a prominent nucleolus and coarse chromatin granules. The membrane surrounding these cells is composed of a layer of squamous cells covered by a thin cuticle. The wall of the reservoir and the duct has a layer of squamous cells lined by a wrinkled intima.

Discussion

The adult has an infrabuccal chamber while the pupa has an anterior recess in that region. The epithelium of the buccal tube and the pharynx consists of squamous cells in the adult and cuboidal or low columnar cells in the pupa. The pharynx of *A. gracilis* resembles in structure the Old World doryline *Anomma wilverthi* (Bugnion, 1930), and in general histology the New World *Eciton* (Whelden, 1963) and *Cheliomyrmex morosus* (Gotwald, 1971). However, variations are seen in the arrangement of spines along the inner surface.

The epithelium of the postpharyngeal glands is folded in the pupa of *A. gracilis* and not so in the adult.

The oesophageal epithelium of the pupa of *A. gracilis* has smaller folds and the lumen is wider when compared to the adult. The long, acute spines reported in the queens and workers of two species of *Eciton* (Whelden, 1963) are absent here.

A crop and proventriculus generally present in ants between the oesophagus and ventriculus are absent in *A. gracilis* and in the Old World *D. labiatus*. Eisner (1957) described the proventriculus in *E. hamatum* as degenerate. Whelden (1963) has reported a difference in the position of the small crop in queens and workers of two species of *Eciton* (*hamatum* and *burchelli*), and the presence of a small proventriculus in both species. In the

worker of *C. morosus* the crop and ventriculus lie juxtaposed and are connected by a reduced membranous proventriculus (Gotwald and Kupiec, 1975). There is no mention of a cardiac valve at the posterior end of the oesophagus in *D. labiatus* (Mukerjee, 1926). A simple cardiac or stomodaeal valve is reported to be present in *E. hamatum* (Eisner, 1957) and in *C. morosus* (Gotwald, 1971). In the adult and pupa of *A. gracilis* the posterior end of the oesophagus continues into the ventriculus and forms a cardiac valve; this valve is shorter in the pupa.

The ventriculus of the adult and pupa of *A. gracilis* resembles in general form that of the ponerine male, *Rhytidoponera metallica*, (Hagopian, 1963) in having a dorsal concavity in its posterior half. The New World doryline *C. morosus* worker has a tubular posterior portion that is referred to as the pre-Malpighian tubule tract (Gotwald, 1971). This has not been reported in any of the other species described (Mukerjee, 1926; Whelden, 1963). The ventricular epithelium of the adult of *A. gracilis* is composed of large columnar digestive cells and small, scattered, pyramidal regenerative cells. In the pupa, however, three types of digestive cells, each restricted to a region of the ventriculus, were recognized, and these represent stages in the maturity of the epithelium.

A pylorus that is divided into anterior and posterior portions by an inward fold of the epithelium is present in the adult and pupa of *A. gracilis*. This is indicated as a pyloric constriction in *D. labiatus* (Mukerjee, 1926). Such a pylorus is not reported in the New World species described (Whelden, 1963; Gotwald, 1971).

The intestine is a tube of uniform diameter in all ants described. In *D. labiatus*, however, it is reported to be divisible into an anterior narrow ileum and a posterior broader colon (Mukerjee, 1926).

At the junction of the intestine and the rectum a rectal valve with a sphincter is present in the adult and pupa of *A. gracilis*. A structure comparable to this has not been reported in any of the other dorylines described (Gotwald, 1971; Mukerjee, 1926; Whelden, 1963). There seems to be no consistency in the number of rectal pads or papillae; small rectal glands in *D. labiatus* male (Mukerjee, 1926), usually 3 and rarely 6 in *Eciton* workers and frequently 6 and infrequently 3 in *Eciton* queens (Whelden, 1963); 2 lateral papillae in the worker of *C. morosus* (Gotwald, 1971). The present investigation revealed the presence of 3 rectal pads in the adult and pupa of the male, two lateral and one ventral.

Maxillary glands situated on either side of the infrabuccal chamber and opening into the posterior part of the buccal tube have been reported in the male ponerine ant, *R. metallica* (Hagopian, 1963), in the queens and workers of the two species of the New World doryline, *Eciton* (Whelden, 1963), and in the workers of a New World doryline, *C. morosus* (Gotwald and

Kupiec, 1975). These glands are not present in adults and pupae of the male *A. gracilis*.

There are 18–20 Malpighian tubules in the adults and pupae of the male of *A. gracilis*. Mukerjee (1926) has reported the presence of numerous tubules in the male of *D. labiatus*. Analysis of the Malpighian tubule count made by Gotwald (1971) indicates that the range in number of tubules in workers is less species specific. However, the mean numbers of tubules are distinct for several species and he assumes that they could be correlated with the body size; a higher mean for the larger *Labidus* species, and a lower mean for the smaller *Neivamyrmex* species. The present count of 18–20 for one of the smallest of the dorylines, *Aenictus*, does not support Gotwald's assumption.

Salivary glands and gland ducts in the adult and pupa of *A. gracilis* are very small and interspersed in fat cells. The glands are simple branched acinar glands, and the ducts are typical in being straight with a tortuous lumen. In the other dorylines described these glands are of different types; short, thick, and branched tubules in *Eciton* workers and queens (Whelden, 1963), and small cylindrical lobes in workers of *C. morosus* (Gotwald, 1971).

Whelden (1963) reported much variation in shape and in size of the mandibular gland and the reservoir in the two species of *Eciton*. In the males of these species he describes the posterior end of this gland as being frequently bifurcate, the two branches passing one above, the other below the optic nerve. The number of secretory cells in these glands varies from 100 to 1400. The mandibular gland in *C. morosus* (Gotwald and Kupiec, 1975) is composed of a few irregularly-shaped cells with distinct nuclei; a reservoir was not reported. The glandular portion of *A. gracilis* resembles in all respects that of the ponerine, *R. metallica*, (Hagopian, 1963). *A. gracilis* has a reservoir into which the cellular ductules and the intercellular spaces of the glandular portion open.

Gotwald and Kupiec (1975), analyzing the existing information on the morphology, behavior and geographical distribution of the doryline tribes indicate that the subfamily Dorylinae as presently constituted, is triphyletic. The three lineages are the Ecitonini-Cheliomyrmecine, the Dorylini, and the Aenictini. They advocate the retention of the subfamily Dorylinae to include the tribe Dorylini and make a case for the creation of a subfamily Ecitoninae already introduced by Brown (1973) to include the tribes Ecitonini and Cheliomyrmecini. The status of Aenictini, they conclude, remains to be determined by further investigation.

The present investigation of the anatomy and histology of the digestive system has brought to light several features of phylogenetic importance. In the absence of a crop, a proventriculus, and maxillary glands, *Aenictus* is distinctly different from the New World forms. The presence of a dorsal concavity in the posterior half of the ventriculus, the pylorus internally

divided into anterior and posterior portions, and the presence of a rectal valve with a sphincter are the unique features exhibited in the digestive system of *Aenictus*. These structures lend support to the elevation of the tribe Aenictini to a subfamily rank, and add to the concept of the triphyletic origin of the dorylines.

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Department of Biological Sciences, Fordham University, Bronx, NY 10458.

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FECELIA BIORBIS N. SP. (HETEROPTERA: PENTATOMIDAE),
A NEW SPECIES FROM HAITI

Joseph E. Eger, Jr.

Abstract.—A third species of *Fecelia*, *F. biorbis* n. sp. from Haiti, is added to the genus. It is described, figured and compared to the other species of *Fecelia*.

The genus *Fecelia* Stål, 1872, includes two previously described species, *F. minor* (Vollenhoven, 1868) and *F. nigridens* (Walker, 1867). It was recently revised by Grazia (1976); however, a single distinctive specimen in the collection of the American Museum of Natural History was not included in her work. This specimen represents a new species and is described here.

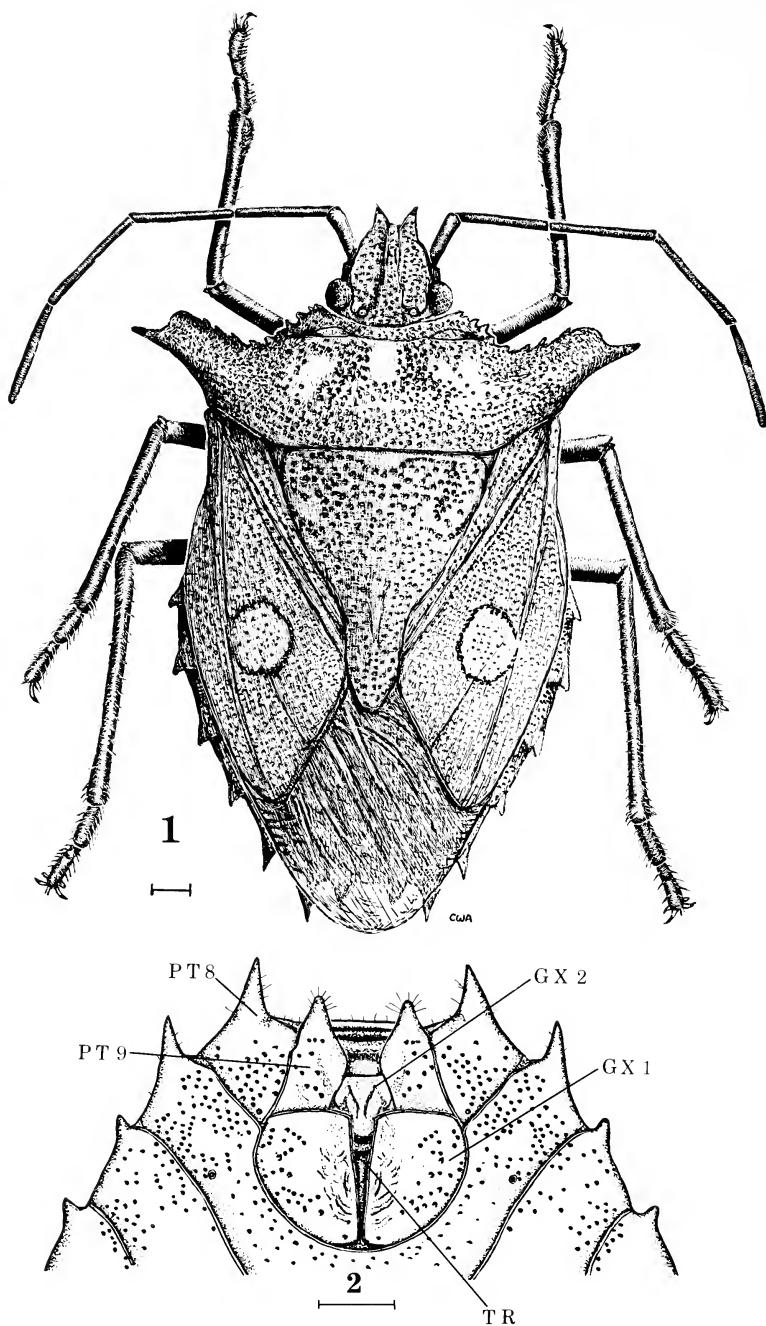
Fecelia biorbis n. sp.

Color above chestnut brown, scutellum somewhat lighter. Punctuation dense, irregularly distributed, concolorous or piceus (Fig. 1). Venter similarly colored; punctuation dense, piceus. Body length with membranes 18.6 mm.

Head 3.4 mm wide across eyes, 3.3 mm long at meson, evenly punctured, transversely rugose. Juga strongly surpassing tylus, divergent anterior to tylus; apices acute. Vertex flat, interocular width 2.2 mm. Antennal segments 1-4 nearly concolorous with dorsum, slightly red-tinged; last segment lighter; first segment reaching apex of jugum; length of segments 1-5: 1.5; 2.4; 2.7; 2.9; 2.6 mm. Bucculae toothed anteriorly, evanescent posteriorly. First rostral segment surpassing bucculae by approximately $\frac{1}{5}$ length of segment; second segment extending nearly to anterior margin of mesocoxae; third segment reaching posterior margin of metacoxae; apex of rostrum extending to middle of third visible abdominal sternite.

Pronotum 3.6 mm long at meson; width between apices of humeri 12.5 mm; disc with broad longitudinal band devoid of punctuation, outlined by punctuation. Two roughly circular, lightly punctured maculae present posterior to cicatrices, separated from latter by band of moderately dense punctuation, these maculae outlined by piceus punctuation. Cicatrices with distinct tubercle, lightly punctured near tubercle. Humeri strongly developed, abruptly narrowing near apex into acute spines, densely punctured above. Anterolateral margins strongly concave, denticulate.

Scutellum 5.0 mm wide at anterior margin, 6.4 mm long at meson. Punctuation large and irregularly distributed at base, becoming smaller and more



Figs. 1-2. *F. biorbis*. 1. Dorsal aspect; 2. Female genital plates; first gonocoxae (GX1), second gonocoxae (GX2), eighth paratergites (PT8), ninth paratergites (PT9), triungulum (TR). Dimensional lines equal 1 mm.

evenly distributed posteriorly, piceus on roughly anterior third of scutellum and posteriorly near apex. Margin of basal angles and anterior $\frac{1}{4}$ of lateral margins piceus.

Each corium finely and densely punctured, punctation becoming somewhat smaller and more dense posteriorly; with small, evenly distributed concolorous calli. Each corium with large, central piceus ring surrounding nearly circular macula, the latter only lightly and shallowly black punctured. Posterior margins convex, with finely broken submarginal piceus line.

Each connexivum strongly exposed; piceus punctation most dense anteriorly on each segment. Width of abdomen at widest point 9.8 mm.

Prosternum weakly sulcate; mesosternum carinate; metasternum flat. Ostiolar rugae spatulate, extending roughly $\frac{1}{4}$ distance from inner margin of ostiole to outer metapleural margin. Legs with femora acutely toothed on superior face at apex; superior face of tibiae flat or very shallowly sulcate. Second to fifth visible abdominal sternites broadly and shallowly sulcate mesially. Length of visible sternites 2–6 at meson (first segment not visible mesially): 0.8; 1.1; 1.4; 1.4; 2.0 mm. Postero-lateral angles of segments 2–5 provided with small acute tooth; this tooth becoming more elongate and spinose on segment 6.

Mesal margins of first gonocoxae with acute apices, narrowly separated at base, diverging posteriorly, exposing triangulum and extending onto second gonocoxae. Length of first gonocoxae 1.7 mm, width at widest point 1.6 mm. Eighth paratergites acutely spinose posteriorly; ninth paratergites rounded posteriorly (Fig. 2).

Holotype.—Female, labelled (a) Furcy, 4000'; Haiti VII-10-56; B&B Valentine. (b) Sweeping in bushy ravine. (c) Haylini. Deposited in the American Museum of Natural History, New York, N.Y.

Distribution.—Haiti.

Comments.—This species basically agrees with Grazia's description of the genus and resembles its congeners in the length and shape of the ostiolar rugae, the presence of apical femoral spines, and the median furrow which occurs on the basal abdominal sternites. It is most closely allied to *F. nigridens* and agrees with this species in size, shape of the female genital plates, and in the acute, divergent juga. The single representative of the species described here is sufficiently distinct that dissection of the genitalia was not deemed necessary. *F. biorbis* can be readily distinguished from the two other species of this genus by the abruptly narrowed humeri and the piceus ring on each corium.

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Dept. of Entomology, Texas A&M University, College Station, Texas 77843.

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ABSTRACTS OF PAPERS PRESENTED AT THE
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Migration, distribution, and habitat preferences of *Blattella germanica* (L.) in urban, low-income apartments (Dictyoptera: Blattellidae). R. C. Akers and W. H. Robinson, VPI and State Univ., Blacksburg, VA 24061

This study monitored the dispersal behavior and determined density distribution and habitat preferences of *B. germanica* in 3 urban, low-income apartment buildings. Three traps (1-qt. jars) were placed in the kitchen, pantry, and bathroom of each apartment. Two hundred nymphal and virgin adult phenotypic mutant German cockroaches were released into established apartment building populations and trapped at weekly intervals. Trapping proved that this insect could migrate between apartments and integrate with the existing population. Trapping disclosed that the existing German cockroach population was not distributed evenly throughout the buildings. In each building at least one location (=apartment) the number of captured cockroaches was significantly greater than at any other location. In bldg. A, 80% of total cockroaches captured were from apts. 4 and 5; bldg. B, 75% were from apt. 1; bldg. C, 55% were from apt. 6. This focal location corresponded to the apartment with the most severe sanitation problem. Habitat preferences differed at the trapping sites in the 3 buildings: bldg. A, kitchen—22%, pantry—39%, bathroom—39%; bldg. B, kitchen—21%, pantry—37%, bathroom—42%; bldg. C, kitchen—41%, pantry—21%, bathroom—38%. The German cockroach dominated other cockroach species in the urban, low-income apartments studied. Laboratory-reared cockroaches were able to disperse and integrate with the established population.

Comparative toxicity of etrimfos to gypsy moth larvae and house flies. M. Akram and A. J. Forgash, Dept. of Entomol. and Econ. Zool., Rutgers Univ., New Brunswick, NJ 08903

Etrimfos (*O-O*-dimethyl-*O*-(6-ethoxy-2-ethyl-4-pyrimidinyl) phosphorothioic acid ester), a new organophosphate insecticide was tested against 2nd, 3rd, 4th, and 5th instars of gypsy moth larvae (*Lymantria dispar* L.) and susceptible and multi-resistant strains of adult house flies (*Musca domestica* L.). For each dosage, 50 insects were tested in five replicates containing 10 insects per replicate. Etrimfos was applied in acetone solution to the thoracic dorsum with a microapplicator. Results showed an increased

tolerance of gypsy moth larvae to this chemical with larval growth. Individuals of the 3rd-, 4th-, and 5th-instars can tolerate up to 2.6, 5.2, and 28.8 times as much as 2nd-instar larvae. In gypsy moth an active microsomal oxidative system has been reported, presumably, the increase in tolerance to etrimfos of later instars is related to the changes in activity of the mixed-function oxidases. Two susceptible strains (WHO/IN and Wilson) of house fly showed a relatively high sensitivity to etrimfos. However, Es and A strains, which were cultured under the pressure of resmethrin and diazinon, respectively, were 4.5 and 14.2 times tolerant to this compound. Multiresistance to insecticides as the result of selection with a single material is well recognized; presumably, diazinon selection was responsible for increased tolerance to etrimfos. The lower tolerance of ES suggests a less developed or different mechanism of resistance than A strain.

Release of oviposition-detering pheromone by apple maggot flies, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae) A. L. Averill and R. J. Prokopy, Dept. of Entomol., Univ. of Mass., Amherst, MA 01003

Following egg-laying into a fruit, the female apple maggot deposits a marking pheromone on the fruit surface which deters subsequent oviposition. Two techniques were developed to accurately quantify the amount of marking pheromone deposited. 1) Dusting a recently marked fruit with dry magnetic toner (Olivetti) used in paper copying machines renders the pheromone trail readily apparent. 2) Feeding ♀♀ amaranth results in a trail which is conspicuously dyed. Pheromone trail length and area are then measured with an ocular micrometer. For 14-day-old ♀♀ ovipositing in 15 cm diameter hawthorns, the average length of pheromone trail was 52.8 mm, the average width .05 mm and the average area 2.7 mm² (N = 99). Old flies produce smaller trails than young flies and starved flies deposit much less material than unstarved flies. There was a low, though significant, positive correlation ($r = +0.315$) between time spent in ovipositor dragging and area of pheromone trail. In individual flies, the degree of variability in pheromone trail area was large among successive dragging bouts within single days. The presence of amaranth dye (internally confined to the digestive tract) in the pheromone trail suggests that a portion of the pheromonally active substances may be released from the digestive tract. Behavioral bioassays of organs of the digestive and reproductive tracts strongly implicate the hindgut (as well as the ovary) as a site of pheromone production or accumulation.

Oviposition response of the horn fly (Diptera: Muscidae) to environmental and manure characteristics, N. P. Bacon, West Va. Univ., Morgantown, WV 26506

Horn fly control efforts have previously been directed primarily at chemical, biological or sterile methods. Little work on behavioral control has been carried out. The purpose of this study was to investigate horn fly oviposition site selection behavior. Horn flies only oviposit on freshly defecated feces (ca. 10 min), and then only on select pats. The responses of the flies to selected environmental, manure and host-fly interaction characteristics were studied on a rural Pennsylvania dairy farm. Fly number response, used to assess oviposition preferences, indicated that manure pats which were defecated in areas of full sunlight, and on grass or soil substrates attracted the largest number of flies. Pats which were large in size (22.8^+ cm), tall in height (4.3^+ cm), and had features which gave topographic relief to the pat (e.g. edge, cracks, depressions) also increased fly response. The expression of these topographic features was found to be dependent on substrate, pat moisture content, and pat height. Fly response was least when manure pats were defecated under roofed areas, at night, on liquid substrates, on pats with small height-size ratios, and on pats which lacked topographic relief features.

These results offer another avenue of investigation for biological control of the horn fly.

The impact of the soil systemic, aldicarb and the foliar insecticide, pirimicarb on potato plant growth. B. A. Bajusz, Z. Smilowitz, T. P. Mack, F. L. Petitt, C. A. Martinka, and M. E. Whalon, Pesticide Res. Lab., Pennsylvania State Univ., University Park, PA 16802

In field experiments designed to evaluate the impact of an insect pest on crop growth, different application rates of insecticides are often applied to obtain insect populations of different levels. However, to accurately evaluate the insect component the impact of these insecticides on the growth of the plant must be known. A field experiment designed to assess the effect of different green peach aphid, *Myzus persicae* (Sulzer), densities on plant growth was expanded to include tests on the impact of the foliar insecticide pirimicarb and soil systemic aldicarb on plant growth and development. The data indicated that both compounds appear to affect potato growth and development. Pirimicarb applied on a weekly basis to fields containing five aldicarb rates, 0–35 lb ai/A, reduced foliage biomass throughout the season but did not appear to affect tuber biomass. Aldicarb appeared to prolong the period of haulm growth and increasing soil dose delayed plant senescence. The effects observed with increasing aldicarb concentrations closely

paralleled those associated with decreasing aphid densities, and could have erroneously been attributed solely to differing aphid numbers. Further experimentation is currently underway to increase our understanding of these findings. It was concluded that the effects of chemical insecticides on plant growth must be known before they are used in plant growth experiments to manipulate insect population size.

Effect of electromagnetic devices on subterranean termites (*Reticulitermes*), drywood termites (*Incisitermes minor*), and German cockroaches (*Blattella germanica*). R. Beal, U.S.F.S. Gulfport, MS 39501, M. Rust and D. Reiersen, U. of Cal., Riverside, CA 92521, D. S. Dalton U.S.E.P.A., Wash. DC 20460 (proj. off.)

There has been a recent increase in the sale of "electromagnetic" pest control devices for use against pest insects and rodents in private homes and in commercial and industrial sites. EPA grants to 2 institutions tested the efficacy of three devices. Field tests with subterranean termites exposed to the devices in Mississippi for 6 months showed no significant effect on tubing activity or frequency of stake attack. Field tests in roach infested apartments in Los Angeles showed no measurable differences in control of roach populations between exposed and unexposed buildings. Lab tests with roaches showed no measurable differences on behavior of roaches in a repellent/nonrepellent choice box situation. In addition, starting with either adult or nymphal roaches there was no significant difference in the resultant number of roaches after 12 weeks of exposure to the devices. Devices had no effect on egg capsules of *Periplanta americana*. In lab tests with drywood termites, no significant differences were found in mortality, amount of wood consumed, or increase in termite biomass after a 3 month exposure to the devices. As a result of these tests and tests against 3 rodent species, EPA initiated enforcement action under the Federal Insecticide, Fungicide and Rodenticide Act to stop the distribution of these devices because of false and misleading claims.

The effects of mowing on the guild of sap-feeding insects associated with Kentucky bluegrass. Richard A. Bean and Robert F. Denno, Department of Entomology, Univ. of Maryland, College Park, MD 20742

Four species of Auchenorrhyncha dominate the sap-feeding guild of insects associated with Kentucky bluegrass. They are in decreasing order of abundance, *Psammotettix lividellus* (Zetterstedt), *Graminella nigrifrons* (Forbes), *Doradora stylata* (Boheman) (Cicadellidae), and *Delphacodes luteulenta* (Van Duzee). The densities of these sap-feeders were measured in mowed (cut monthly) and uncut plots throughout the year to test the effects

of disturbance and habitat modification on the structure of the guild. *G. nigrifrons* is a fugitive species colonizing plots as adults in spring developing a single generation and then emigrating in June. This species achieved equal densities in both uncut and mowed plots. *D. lutulenta* and *D. stylata* are residents and overwinter as adults and nymphs respectively. Adults of these species are mostly brachypterous and significantly lower densities occurred in the mowed plots. The adults of the resident leafhopper *P. lividellus* are macropterous and occurred at equal densities in cut and control plots. Fugitive species were least affected by mowing followed by macropterous residents. The densities of species that are closely tied to resources (brachypterous) were most affected by habitat perturbation.

Sweet corn insect pest management in New Hampshire. J. S. Bowman and A. T. Eaton, Univ. of New Hampshire, Durham, NH 03824

A modification of the New Jersey sweet corn IPM program has been of economic value to participating growers for the past 3 seasons (1977–1979). The program is based upon utilizing grower personnel trained to scout fields for European corn borer and fall armyworm feeding injury and operate black light traps to detect corn earworm moth populations. The results of whorl stage treatments of granular and spray treatments at 15% leaf feeding damage demonstrated economic control of first brood European corn borer with Dyfonate 10GK at 1.5 lb. ai/A or Furadan 10G at 1.0 lb. ai/A applied as single treatments or two applications (5 days apart) of Penncap M 2F at 0.5 lb. ai/A. Promising results have also been obtained with Pounce 3.2EC at 0.1 lb. ai/A and Orthene 75S at 1.0 lb. ai/A. During 1977 and 1978 the late arrival of the corn earworm moths along with low late season populations resulted in savings of two to five applications of pesticides for an average value of \$18.38 per acre. The number of participating growers has increased from three in 1977 to ten in 1979 representing 16 percent of the total sweet corn acreage in New Hampshire. Problems associated with this grower-operated program include difficulty in training personnel to identify light trap catches as well as data gaps in scouting reports and light trap catches when traps are inadvertently not operated. Also, an unreliable source of black light traps has created problems in bringing new growers into the program.

Bait sampling for white grubs (Coleoptera: Scarabaeidae) and wireworms (Coleoptera: Elateridae) in Virginia corn land. S. P. Briggs and W. A. Allen, Dept. of Entomol., VPI and State Univ., Blacksburg, VA 24061

Nineteen fields in two Virginia counties were used to confirm a solar baiting technique for wireworms. In Westmoreland County, Virginia, eight

fields in a corn-small grain-soybean rotation and five in a corn-corn agro-nomic system were tested. In Montgomery County, Virginia, six fields in a corn-corn system were used. The bait consisted of 30 cc of a corn-wheat mixture (1:1 ratio) buried 15.0 cm deep and covered with black and clear plastic. Baits were retrieved after remaining in the field for 14–15 days and all wireworms and white grubs were collected. In addition to baiting, 40 cylindrical soil samples (20.3 cm diameter, 38.0 cm deep) per field were taken to correlate relative sample (bait) populations with absolute sample (core) populations.

A list of the white grub and wireworm species found was established. The baiting technique is shown to be effective on both white grubs and wireworms in Virginia.

Toxicity of the IGR L7063 to *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) and two associated parasites. J. R. Brushwein and J. Grannett, Univ. of Maine, Orono, ME 04469

Laboratory tests of Insect Growth Regulators (IGRs) have demonstrated high levels of toxicity to the spruce budworm, *Choristoneura fumiferana*. Field studies have indicated potential use of IGRs for spruce budworm control programs. Our purpose was to determine comparative toxicities of L7063 to spruce budworms and two associated hymenopteran parasites *Apanteles fumiferanae* Vier. (Braconidae) and *Glypta fumiferanae* (Vier.) (Ichneumonidae). Overwintering budworm larvae on white spruce were collected in the laboratory. Emerged second stage budworms were reared on artificial diet until just prior to the instar tested. Newly molted, unfed 4th and 5th stage budworms were fed artificial diet containing L7063 until larval mortality or parasite emergence. Concentrations of L7063 in diet ranged from 0.063–2.4 ppm. The LC_{50} for field collected, unparasitized budworms was between 0.063 and 0.10 ppm. Larval *A. fumiferanae* and *G. fumiferanae* mortality was determined by dissection of L7063 killed hosts. Parasitism rates of *A. fumiferanae* and *G. fumiferanae* were determined by host dissections and by numbers of emerged parasites. Parasitism rates for eight experiments ranged from 4.6 to 27.9% and 2.9 to 12.9% for *A. fumiferanae* and *G. fumiferanae*, respectively. For all L7063 concentrations tested, little mortality occurred in stage 1 and 2 *A. fumiferanae* larvae or stage 1, 2, and 3 *G. fumiferanae* larvae. Diet concentrations of L7063 between 0.42 and 2.4 ppm caused mortality of all 3rd stage *A. fumiferanae* with death occurring before emergence from the host.

Status of a biological control program against the cereal leaf beetle, *Oulema melanopus* (L.) (Coleoptera: Chrysomelidae). T. L. Burger, USDA, APHIS, Cereal Leaf Beetle Lab., Niles, MI 49120

The cereal leaf beetle, *Oulema melanopus* (L.), an Eurasian pest of small grains, was first observed in the United States in 1959 in Berrien County, MI. Aided by the prevailing winds, its range has expanded primarily to the East to include 20 states and one Canadian province. Through a cooperative Federal and State program five hymenopterous parasites: *Tetrastichus julis* (Walker); *Diaparsis carinifer* (Thomson); *Diaparsis* n.sp.; *Lemophagus curtus* (Townes); and *Anaphes flavipes* (Foerster) have been introduced as an attempt at multiple species biological control of this pest. To date one or more of these parasites have been released and/or recovered in 18 states and one Canadian province. Results obtained from monitoring sites in states where the program was first initiated, revealed high rates of parasitization of eggs and/or larvae of the pest. Overall seasonal egg and larvae parasitization rates of 70 and 90 percent respectively recorded from low, medium, and high host densities. States, such as MI, IN, OH, PA, and NY, which experienced economic damage over moderately large areas in the past, no longer have significant pest populations where high parasitization rates had been encountered for one to two years. To date no single species of the introduced parasites has exhibited dominance throughout its established range in the United States. States are now in the process of assuming total responsibility for the program.

Growth and survival of *Hylotrupes bajulus* (L.) larvae under favorable and unfavorable conditions (Coleoptera: Cerambycidae). K. F. Cannon and W. H. Robinson, Dept. of Entomol., VPI and State Univ., Blacksburg, VA 24061

Hylotrupes bajulus (L.), the old house borer, is unique among Cerambycids in that it can survive and reproduce in seasoned softwoods. Larvae bore just under the surface, hollowing out the outermost layer of wood before continuing deeper into the wood. Larvae seldom break the surface, thus preventing early disclosure. Detection in wood does not usually occur until larvae are nearly full grown or adult insects emerge. Severity of damage produced by this pest is linked to the developmental time of the larvae; it can live and feed up to 10 years in structural wood. Previous investigations and reports of *H. bajulus* in the U.S. have relied on European data and field observations. The data presented here are based on a laboratory colony and controlled field experiments of *H. bajulus* in Virginia. The experiment was designed to study feeding, growth, and survival of *H. bajulus* under favorable and unfavorable environmental conditions. Results of the feeding

and growth studies reveal that under field and laboratory conditions small (2.8–86.6 mg) larvae consume more wood per mg body weight than medium (106.7–197 mg) and large (208.5–430.9 mg) larvae. Excrement (frass) is proportional to consumption. Wood consumption and weight gain are influenced by climatic conditions. Larval survival was not affected by climatic conditions during the duration of the experiment.

Fungicidal inhibition of *Beauveria bassiana*, a pathogen of the Colorado potato beetle (*Leptinotarsa decemlineata* Say.) (Coleoptera: Chrysomelidae). R. A. Clark, Dept. of Plant Path. and Entomology, Univ. of Rhode Island, Kingston, RI 02881

Fungicides used to control *Phytophthora infestans*, the late blight pathogen, may limit the development of epizootics of *B. bassiana* in CPB populations. Using agar-diffusion, 3 fungicides were bio-assayed for inhibition of *B. bassiana*. Plates were inoculated with a spore suspension of 10^6 spores/ml. Paper discs treated with fungicide were placed on the plates. Plates were incubated 5 days at 25 C. Inhibition zones indicated *B. bassiana* was inhibited by 3 fungicides. The insecticide azinphos methyl (Guthion) also had a synergistic effect with at least one fungicide.

To refine quantification of the degree of inhibition, the fungus was grown in Emerson's Broth with doses of the pesticides added to the medium. Flasks were incubated on a rotary-shake table at 25 C. For 7 days, at 24-hr intervals, the contents of the culture flasks were filtered, the mycelial mat dried and weighed. Although conventional fungicides (Manzecob, metiram, chlorothalnil) retarded mycelial growth rate, the late blight specific experimental CGA 48988 had little effect and thus holds the most promise for use in integrated pest management for potatoes.

Insemination frequency and sperm precedence in the German cockroach (Dictyoptera: Blattellidae). D. G. Cochran, VPI and State Univ., Blacksburg, VA 24061

A question of fundamental importance to insect reproductive biology is how frequently a female can be effectively inseminated. The problem can best be approached by use of genetic-mutant markers which allow positive proof of parentage. Using the recessive marker rose eye (*ro*), it has been shown that adult female German cockroaches, *Blattella germanica* (L.), can mate effectively with more than one male. The most common period for remating is between production of successive egg cases, but remating also took place between the first mating and production of the first egg case. In the first instance remating occurred in about 20% of the females studied while in the second instance remating was rare.

Because the German cockroach female normally produces only 3 or 4 egg cases, the later ones with reduced numbers of progeny, the total impact of second matings on all progeny produced tends to be small. That impact is further diminished by the prevalence of incomplete sperm precedence which allows sperm from the first mating to function even after a second successful mating. These results show that monogamy is common in this species, but that superimposed upon it is the willingness of the female to remate occasionally. Presumably remating is opportunistic and occurs in response to sperm depletion in the spermatheca.

Parahost behavior of adult *Gasterophilus intestinalis* (DeGeer) (Diptera:Gasterophilidae). S. E. Cope and E. P. Catts, Dept. of Entomol. and Appl. Ecol., Univ. of Delaware, Newark, DE 19711

In Delaware adult horse bot flies occur from mid June to mid October. Adult activity was closely observed in the vicinity of grazing equines. Individual flies were followed by a mark and release method. The onset of daily parahost activity was correlated to temperature. Males hover intermittently around hosts during the mating period and are rarely seen after mid day. Male flies also defend single or clustered horses from other males through the use of audible encounters and aggressive pursuit. Female fecundity approximated 1000 eggs. The majority of oviposition was completed by mid day and the egg-laying pattern varied in location and concentration. Females are capable of ovipositing the full egg complement in less than 1 hour and exhibit a broad range of tolerance to environmental conditions. Flight characteristics of females are indicative of physiological age. Longevity of adults in their natural habitat is 1–2 days. Adults which were captured in the field and held under laboratory conditions lived for a slightly longer period of time. These studies represent an advance in the knowledge of the biology of *Gasterophilus intestinalis* and help to establish a basis for future experimentation with regard to the development of trapping devices as a method of augmenting host treatment as a control measure.

USDA Procedure for acting on new pest problems. R. L. Cowden, USDA, APHIS, PPQ, Hyattsville, MD 20782

Of the economically important pests that occur in this country, most have come in from foreign sources. With the current widespread interest and concern in pesticides, environmental pollution, and energy conservation, early detection and decision as to what should be done has become increasingly important. It is the function of the New Pest Work Group to review available data and make recommendations to the Deputy Administrator of the Animal and Plant Health Inspection Service as to the best courses of

action concerning newly reported plant pests. Upon detection of a new insect species of pest potential, a determination is made of its probable economic importance in this country. Experts from various Federal and State agencies, universities, industry, and others are called together to discuss and provide advice on future courses of action. Most new species detected are likely to be of little economic importance. A second group may cause concern because of the uncertainty of their pest potential in this country. Thirdly, there are others which are known economic pests on crops or in situations similar to those in the area where they are detected. In the latter two categories, the temporary quarantines, control or eradication, parasite introduction, crop destruction, and other options are considered when recommending action.

Herbivorous insects causing mortality of pine seedlings in an old field. W. J. Cromartie, M. A. Rivera, J. Gfrorer and D. Maser, ENVL, Stockton State College, Pomona, NJ 08240

As part of a study of establishment of Pitch Pine (*Pinus rigida*), seedlings 1-8 yr old in an abandoned agricultural field were censused, tagged and sampled during two years. Percentage defoliation was estimated in spring, summer and fall, 1978, and measured in spring, 1979, on a sample of 30 trees. The principal defoliator was the Red-headed Pine Sawfly (*Neodiprion lecontei* Fitch). Damage by shoot borers (mainly *Rhyacionia* sp.) and sucking insects, including a scale (*Toumeyella* sp.) and aphids (*Cinara* sp.) was also estimated. Intensity of herbivore attack was variable from tree to tree. Thirty-five percent were killed or severely stunted by defoliation or loss of numerous shoots to tip moths. Some trees, however, were virtually unaffected, even when they were adjacent to trees that were killed. Defoliation levels increased from 1978 to 79, except on trees that were 90% defoliated prior to spring, 1978; these showed signs of recovery. A correlation was found between foliar concentrations of potassium and level of defoliation. It is hypothesized that a positive feedback mechanism is responsible for the pattern of herbivore attack on young Pitch Pine.

Geographic variation in vagility in the milkweed beetle, *Tetraopes tetraophthalmus* (Forster) (Coleoptera: Cerambycidae). M. A. Davis, Dartmouth College, Hanover, NH 03755

This study shows that extensive variation in flight and migratory behavior exists within and between *Tetraopes* populations. The vagility of milkweed beetles in different populations in New England was compared by flight testing the beetles with a still air tethering device.

The vagility of populations varied seasonally, with peak vagility coincid-

ing with the peak flowering period of its host plant. Most beetles tested were relatively sedentary, although each population possessed a certain proportion of beetles that were highly vagile. Populations differed significantly in the proportion of highly vagile beetles they contained. It is hypothesized that this geographic variation in vagility is due to differences in the age and remoteness of milkweed patches throughout the range of *Tetraopes*.

Factors affecting honey bee *Apis mellifera* L. (Hymenoptera: Apidae). Foraging on birdsfoot trefoil (*Lotus corniculatus*). G. L. DeGrandi and C. H. Collison, Penn. State Univ., University Park, PA 16802

Honey bees are essential for commercial seed production of birdsfoot trefoil because of self-sterility and incompatibility systems that make cross-pollination necessary. Six commercial varieties, Dawn, Empire, Mackinaw, Missouri-20, Kentucky-Ecotype, and Viking were evaluated for flower production, nectar secretion, and attractiveness to honey bees. Nectar was removed from one-day-old florets with a micropipette and sugar concentration determined with a Baush and Lomb refractometer. Both greenhouse and field studies of first year growth were conducted simultaneously. The total volume of nectar and sugar concentration between varieties did not differ significantly at the 0.05 level of probability in either study. Flowers contained between 0.21–0.25 μ l of nectar, and had a sugar concentration of 14.6%–17.5%. Significant differences were found in flower production, with Empire producing the most florets (mean of 497/10 plants) throughout the season. Viking and Kentucky-Ecotype were the first to bloom, and averaged the least, 21 and 48 florets, respectively. No significant differences were found between Missouri-20, Dawn, or Mackinaw, with each averaging between 88–99 florets. Flowering and attractiveness to honey bees was significantly correlated, with Empire plots having the greatest foraging activity and Viking plots the least. Missouri-20, Dawn, and Mackinaw were equally attractive, but were not foraged as heavily as Empire.

The mayfly fauna (Ephemeroptera) of two Connecticut streams. P. J. Dodds, Univ. of Connecticut, Storrs, CT 06268

The life histories and ecological relationships of mayflies inhabiting two Connecticut streams were studied. Forty-eight species were collected from each stream. Ten were selected for life history analysis utilizing head length frequency classes and arbitrary age groups based on wing pad development. This was correlated with adult flight periods to determine temporal partitioning of the habitat. Two basic life history patterns were found. In the first, nymphs appeared in late summer and autumn and grew throughout the winter, emerging in the spring. Nymphs and adults of the second type were

both present in the summer with eggs diapausing for most of the year. Most species showed a seasonal succession with narrow temporal overlap, although species of the genus *Ephemerella* exhibited more significant overlap. The mayfly community as a whole illustrated seasonal changes with greatest differences occurring between the two rivers in early summer and fall. Numbers increased in early spring and decreased thereafter until early summer, when hatching of summer species induced another increase; numbers declined again through the summer months. Species diversity also decreased from spring to fall in both rivers. Such changes in the mayfly fauna were associated with life history phenomena, including delayed hatching, maturation, and adult emergence.

Impact of predators and parasites on the survival of *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae). P. F. Dowd and L. T. Kok, Dept. of Entomol., VPI and State Univ., Blacksburg, VA 24061

Several predators and parasites frequently observed in the vicinity of thistle plants infested by the thistle head weevil, *Rhinocyllus conicus* Froelich, were studied during 1978 to update their impact on *R. conicus*. Potential predators were collected from the flower heads of musk thistle (*Carduus nutans*) in Pulaski Co., VA during the oviposition period of *R. conicus* in the spring. Exposure tests using insects in the families: Cleridae, Cantharidae, Lampyridae, Elateridae, Nabidae, and Formicidae indicated no predation on the eggs and adults of *R. conicus*. However, similar studies with spiders in the families Salticidae and Thomisidae showed predation on the adult weevils and third instars. Salticid spiders appeared to prefer larvae (6.5/wk), while the thomisid spiders were more important predators of adult weevils (3/wk). These spiders, however, were not abundant and thus were not important mortality factors. Parasitism was studied by collecting 50 terminal heads of plumeless thistle (*Carduus acanthoides*) from each of 2 selected sites, and 100 terminal heads and peduncles of musk thistle from each of 3 sites during early summer. Twenty percent of the heads were dissected soon after collection and those remaining were held for parasite emergence. Four species of parasites were recovered, 2 of which were previously reported on *R. conicus*. Rates of parasitization of *R. conicus* in the 2 plumeless thistle sites were 0 and $14.8 \pm 8.7\%$, as compared to $5.0 \pm 1.8\%$, $1.2 \pm 1.3\%$ and $0.27 \pm 0.55\%$ in the 3 musk thistle sites. The rate of parasitization generally was not sufficiently large to be a major mortality factor of *R. conicus*.

Ovipositional preference of the grape colaspis, *Colaspis brunnea* (Fab.) (Coleoptera: Chrysomelidae) in North Carolina. A. T. Eaton, R. L. Rabb and J. W. Van Duyn, Univ. of New Hampshire, Durham, NH 03824, and North Carolina State Univ., Raleigh, NC 27650

The effects of four different soils on ovipositional preference of the grape colaspis were investigated in field cage and laboratory tests. A 1976 field cage test (RCB design) utilized soybeans growing in caged areas measuring 2.74×1.83 m. A thin layer of test soil occupied the top 3 cm of the soil profile; the caged areas were divided into quadrants for the four soils. Adults of *Colaspis brunnea* were swept from surrounding soybean fields and released inside the cages. After allowing six weeks for oviposition and growth of the larvae, soil samples were taken inside the cages. The number of larvae recovered from the soil demonstrated a preference for clay loam followed by loam, muck, and sand. The former were highly creviced soils; the latter had few surface crevices. The following year, repetition of the test in the field and laboratory gave similar results. The lab test utilized cylindrical plastic containers, 15 cm in diameter \times 4 cm deep, into which 10 male and 10 female *Colaspis* were placed. After several days, eggs were carefully recovered from the soil, and the number of eggs recovered in each quadrant (soil type) were compared. Additional testing with the same containers demonstrated a preference for creviced soil over smooth soil. Further laboratory observations suggested that adults preferred to oviposit in areas of low light intensity.

Presocial behavior in *Cerceris watlingensis* Elliott & Salbert (Hymenoptera: Sphecidae). N. B. Elliott and T. Shlotzhauer, Hartwick College, Oneonta, NY 13820

Earlier studies had shown that females of *C. watlingensis* shared nests. Marked females were observed on San Salvador Island, Bahamas, during November and December, 1978 to determine the extent of nest sharing and switching. Newly emerging females remained in the parental nest for several days. In most cases several females provisioned these nests during this period. After a few days the young females switched to new nests. Nest switching was preceded by a day's searching activity during which females flew restlessly about, often biting the sand's surface. In some cases the new nests may have been freshly dug, but we observed females taking over already established nests. Females always chose new nests at least one meter away from their original nests, although entrances in this species were often only a centimeter apart.

Activities of the individuals in shared nests were compared, and one was always a more effective provisioner. The major provisioner always left the

nest first in the mornings, spent less time in the nest between provisioning trips, and provided more prey per day. The other females spent more time within the nest, often with the head in the entry. This behavior served to guard the nest against enemies, especially ants, the major predators of the species. Thus there is the beginning of division of labor in this species.

Effects of dietary nitrogen on ^{14}C -glycine and ^{14}C -formate incorporation into body urates of *Blattella germanica* (Dictyoptera: Blattellidae). J. A. Engebretson and D. E. Mullins, VPI and State Univ., Blacksburg, VA 24061

The relationship of dietary nitrogen to urate metabolism and the incorporation of two radiolabeled precursors has been examined in *Blattella germanica*. Male and female cockroaches maintained on diets ranging from 0 to 42% protein and injected with either ^{14}C -glycine or ^{14}C -formate were examined for retention of total radioactivity in whole insects and their urate fractions.

Urate synthesis/storage increased in cockroaches maintained on the higher protein diets, whereas urate levels decreased in those insects on low nitrogen diets. Greater radiolabel retention was found in insects maintained on the high protein diet when injected with either ^{14}C -glycine or ^{14}C -formate; however, cockroaches injected with ^{14}C -formate retained almost twice as much radioactivity as those injected with ^{14}C -glycine.

Incorporation of ^{14}C -glycine into the urate pool varied significantly among insects maintained on different dietary regimes. Insects on higher dietary nitrogen levels incorporated more radiolabel into urates. The pattern of ^{14}C -formate incorporation into body urates differed from that observed for ^{14}C -glycine. More radioactivity was found in the urates from insects maintained on the intermediate nitrogen diets. Insects fed a 42% protein diet incorporated significantly less ^{14}C -formate into their body urates. These levels were comparable to those obtained from insects maintained on 0 and 5% protein diets.

Niche relations of stinkbugs (*Podisus* spp.) attacking eastern tent caterpillars. E. W. Evans, Cornell Univ., Ithaca, NY 14853

The importance of interspecific competition in shaping the life history characteristics of insects is presently unclear. The present study addresses the issue by considering patterns of prey exploitation of three species of predatory stinkbugs, *Podisus maculiventris*, *P. placidus*, and *P. modestus* (Hemiptera: Pentatomidae), which were found together, attacking eastern tent caterpillar larvae (Lasiocampidae: *Malacosoma americanum*). Tents of *M. americanum* and more than 500 associated adults of the three predator species were censused in 1977–79 near Ithaca, N.Y. While only *Podisus*

maculiventris adults were found about the tents during the first half of the larval period of *M. americanum*, adults of all three predators were found together about the tents thereafter. During this period of overlap, the three predators did not differ in the sizes of prey they consumed, despite differences in the sizes of these predators themselves. The three predators did differ, however, in their locations: *P. placidus* was most often found inside tents, *P. maculiventris* on the surface of tents or within 30 cm of the tents, and *P. modestus* more than 30 cm from the tents. These results suggest that the three species have diverged in where they hunt for prey. As individual predators readily attack prey already subdued by other individuals, this divergence in site of hunting may reduce interference in consumption of prey, and this may reflect the importance of interspecific competition in determining how these predators exploit tent caterpillars.

Effect of temperature and light on aggregation behavior of *Aedes stimulans* larvae (Diptera: Culicidae) in a woodland pool. G. P. Fernald and J. F. Burger, Dept. of Entomol., Univ. of New Hampshire, Durham, NH 03824

Behavior of *Aedes stimulans* larvae in southeastern N.H. was studied relative to daily changes in water temperature. Observations were made on a 41 × 2.5 m woodland pool divided into 14 sections. Temperature readings and larval counts were taken in each section from initiation of hatching at 2.7°C (March 6, 1979) until adult emergence was complete (May 12, 1979). Maximum vertical and horizontal temperature gradients occurred on bright, sunny days. Maximum surface temperatures occurred over 5 cm deep margins in the shallower sections. Aggregating behavior of *A. stimulans* was a complex response to temperature and incident solar radiation. These were major factors initiating and directing horizontal movement of larvae. Diurnal warming and nocturnal cooling induced the daily formation and dispersal, respectively, of larval aggregations. Vertical and horizontal distribution was more uniform when temperature gradients were low. Larvae were mostly inactive below 5°C except for vertical movement associated with feeding and respiration. Horizontal movement in response to light was greatest at 7–10°C. Above 10°C horizontal movement was a thermotactic response to increasing temperature. Larvae did not cross thermal barriers more than 2°C below temperatures in the aggregation site. Larvae tended to move toward areas of higher temperature until water temperature in shallow sections reached the optimum (18–19°C). Thereafter, larvae tended to avoid areas of higher temperature (>20°C) and seek areas of lower temperature in deeper sections of the pool.

A definitive method for determining pear seedling resistance against pear psylla, *Psylla pyricola* Foerster (Hemiptera: Psyllidae). B. J. Fiori¹ and R. C. Lamb², SEA, USDA, Geneva, NY¹. New York State Agric. Expt. Stn., Geneva, NY 14456²

Reduction of egg deposition and nymphal mortality have been shown to be responsible for resistance against the pear psylla in *Pyrus ussuriensis* and crosses of *P. ussuriensis* with *P. communis*. Exposure of candidate seedlings to unconfined adults and counting the number of nymphs per seedling after appearance of 5th instars (25–30 days) has been suggested and employed to determine resistance. The method does not permit seedling replication in a single test, does not exclude preference and permits some seedlings to escape infestation and remain unclassified. To avoid these serious disadvantages the following method was devised using known resistant and susceptible pear stock grafted to potted rootstock. Dialysis tubing was used to confine 5♂ and 5♀ psylla adults on two leaves of each plant for a 10-day period; tubing and adults were removed, eggs were counted and reduced to 15 per leaf by rubbing. After an additional 15–20 days (appearance of 5th instars) nymphal counts were taken. In 4 tests using 2 plants each of 1 resistant and 2 susceptible stocks, average egg deposition and number of nymphs was reduced 57–83% and 87–100% respectively on resistant stock. Results indicate the number of eggs deposited within 10 days can be used to determine resistance of candidate seedlings, thus reducing testing time from 25–30 to 10 days, and that known resistant and susceptible standards should be included in each test. The method provides for at least 2 replications per seedling, excludes preference and does not allow escapes.

PTTH and ecdysone release in last instar larvae of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae). D. B. Gelman and D. K. Hayes, Insect Reproduction and Livestock Insects Laboratories, USDA, Beltsville, MD 20705

European corn borer larvae were reared under a photoperiodic regimen of 16 hours of light and 8 hours of dark and a temperature of 30°C, conditions which promote pupation. Based on a comparison between % pupation in controls (unligatured larvae) and % pupation or formation of intermediates in ligatured larvae, it was concluded that PTTH release, under the above conditions, begins approximately 24 hours before the formation of the pharate pupa, and that ecdysone release by the prothoracic glands occurs at least 6–9 hours after PTTH release. Both PTTH and ecdysone release as well as the formation of the pharate pupa appear to be rhythmic in that PTTH release and the formation of the pharate pupa are associated with the onset of darkness, while ecdysone release is associated with the onset of

dawn. Ligatured larvae which did not show signs of pupation by 96 hours post ligation never did show such signs, although most remained alive for 30–40 days. This indicated that effective concentrations of PTTH are not released before the 24 hours preceding pharate pupal formation. Since many headless pupae did show adult development, including completely formed wings and legs with scales, it can be concluded that neurohormones and hormones needed for this development and produced by structures in the head have been released before the formation of the pharate pupa.

Effects of decapitation on ecdysone and vitellogenin titers and egg maturation in *Aedes aegypti* (Diptera: Culicidae). J. T. Greenplate, Cornell Univ., Ithaca, NY 14853

Egg development in *Aedes aegypti* is governed by an intricate control system involving several hormones. Early studies were limited to measuring oocyte growth alone. However, recent discoveries have allowed the study of a sequence of intervening steps and products. Early decapitation experiments associated egg maturation with the release of a factor from the head at 4–8 hr after blood-feeding. Later *in vitro* research suggested that a brain hormone (released after blood-feeding) prompts the ovary to secrete ecdysone which stimulates the fat body to synthesize vitellogenin, the yolk protein precursor. *In vivo* support for this scheme has been lacking, but recent studies by this author add such support. *A. aegypti* females were decapitated at various times after blood-feeding. At 20 and 48 hr post blood meal (PBM), the animals were dissected and divided into two groups: females with maturing oocytes (yolk length $> 100 \mu\text{m}$) and females with arrested oocytes (yolk length $\leq 50 \mu\text{m}$). Females maturing oocytes at 20 and 48 hr contained much higher titers of ecdysone and vitellogenin respectively (measured via radioimmunoassay and rocket-immunoelectrophoresis respectively) than did females in oogenic arrest. These experiments agree with early work in which egg maturation in *A. aegypti* was linked to the initial release of a brain hormone. In addition, the association of brain hormone release and egg maturation with the production of large amounts of ecdysone and vitellogenin lends *in vivo* support to the latest *in vitro* studies.

Control of neotenic development in a primitive termite (Isoptera: Hodotermitidae). S. Greenberg and A. M. Stuart, Dept. of Zool., Univ. of Mass., Amherst, MA 01003

Functional reproductives in colonies of the lower termites have been shown to inhibit the precocious sexual development (neoteny) of competent larvae. The mechanism of this inhibition has not been conclusively dem-

onstrated. It has been postulated that this inhibitory influence is exerted through sex-specific non-volatile pheromones that are given off together with the feces of functional reproductives: larvae obtain the postulated inhibitory pheromones by proctodeal feeding. However, no pheromones which inhibit neotenic development in larvae have ever been isolated from any termite species. The hypothesis that the inhibitory pheromones are contained in feces from functional reproductives was tested using the west coast damp-wood termite *Zootermopsis angusticollis* (Hagen) (Isoptera: Hodotermitidae). As expected neotenic reproductive development was inhibited in colonies of larvae that contained a pair of functional reproductives. When filter paper impregnated with feces and hind gut contents from male and female reproductives and larvae were fed to groups of larvae that did not contain a pair of functional reproductives, neotenic development was actually stimulated compared to control colonies fed filter paper only. These results suggest that in the termite *Z. angusticollis*, the postulated inhibitory pheromones are not contained in feces from functional reproductives nor circulated in colonies by proctodeal feeding. Instead, proctodeal feeding may have a primarily nutritive role, in this termite species, as well as being essential for the transfer of symbiotic protozoa.

Resmethrin sprays for relief from deer flies, *Chrysops atlanticus* (Diptera: Tabanidae). E. J. Hansens, Rutgers Univ., New Brunswick, NJ 08903

Resmethrin appeared promising as a safe insecticide which would reduce deer fly annoyance to harvesting crews and other agricultural workers in fields near large salt marsh breeding areas. During two seasons resmethrin EC was applied at 0.025, 0.05, and 0.1 lb/A using conventional air-blast sprayers. Spray was directed from the edge of the fields into the vegetative barrier between these fields and the salt marsh. The sprays were applied between 7:00 and 8:45 a.m. when wind was less than 5 mph. Observations were made before treatment and approx. 1, 4, 8, 24, and 48 hr after treatment both in treated and nearby untreated areas. Effectiveness was measured by averaging 5 counts of flies taken in 10 figure-8 sweeps with an insect net around the observer's head. Pre-treatment counts varied from 15 to more than 200 deer flies/10 sweeps. Dosages of 0.1 and 0.05 lb/A reduced flies visiting a human host by more than 95% at 1 hr post-treatment, by 50-95% after 8 hr and 0 to 85% after 24 hr. Sprays with 0.025 lb/A were nearly as good. For New Jersey only label approval has been obtained for sprays for deer fly control using resmethrin EC applied at 0.025 to 0.05 lb ai/A in agricultural and recreational areas. Such applications can be expected to give greatly reduced deer fly annoyance for 1-2 days.

A field study of *Aedes sollicitans* (Walker) (Diptera:Culicidae) as a vector of filarial worms. W. M. Johnson and W. J. Crans, Mosquito Research and Control, Rutgers Univ., New Brunswick, NJ 08903

Laboratory studies have shown *Aedes sollicitans* to be a susceptible host for the larvae of *Dirofilaria immitis* (Leidy). This mosquito has long been suspected of being a major vector of dog heartworm along the New Jersey coast. To date there has been no direct field evidence to support these findings and infective stage larvae have never been recovered from wild populations. *Ae. sollicitans* were collected from CO₂-baited CDC light traps during the summer of 1978 to determine if filarial worms could be recovered at a site where dog heartworm was known to be endemic. The traps were operated once weekly from June to October at 3 sites along a 3 km transect from a breeding marsh into the upland. *Ae. sollicitans* were anesthetized, sorted and pooled into groups of 150, and infective stage filarial worms were extracted by a modified Baermann technique. Approximately 100 mosquitoes from each collection were individually dissected to detect developing stages of the parasite. Dissections revealed developing filariae as early as June, but infective stage larvae were not recovered by extraction until late August and September. Results showed that natural populations of *Ae. sollicitans* were capable of harboring filarial parasites but suggest that there may be a seasonal distribution in the transmission to vertebrate hosts.

A systematic analysis of the genus *Actia* Robineau-Desvoidy in North America with descriptions of two new species (Diptera: Tachinidae). M. A. Kamran, Dowling College, Oakdale, NY 11769

The genus *Actia* R.-D. consists of small flies which are parasitic on microlepidopterous larvae. They are an abundant group and have a worldwide distribution comprising ca 60 species.

The genus *Actia* was erected by Robineau-Desvoidy in 1830. Over the years its generic limits were invariably given a broad interpretation with the result that hundreds of specimens in various museum collections, loosely ascribed to *Actia* R.-D., in fact did not belong there. Recent authorities have looked at this assemblage much more critically and sharply defined the generic limits of the many taxa included therein.

This paper presents the important diagnostic characteristics of the tribe Siphonini, and all points of discussion relevant to generic limits in the subtribe Siphonina. A key is provided for the separation of all the known North American genera, viz., *Actia* R.-D., *Aphantorhapha* Towns., *Ceranthia* R.-D., *Ceromya* R.-D., *Chaetostigmoptera* Towns., *Peribaea* R.-D., *Pseudosiphona* Towns., *Siphona* Meig., etc.

The genus *Actia* R.-D. is reviewed. Among the recorded North American

species of *Actia*, the following 4 are recognized as valid: *A. autumnalis* (Townsend), *A. diffidens* Currier, *A. interrupta* Currier, and *A. rufescens* (Greene). Two new species, *A. labellata* and *A. pauciseta*, are described. A key for the separation of the North American species is provided.

Removal method estimation of *Blattella germanica* (L.) (Dictyoptera: Blattellidae) populations. C. B. Keil, VPI and State Univ., Blacksburg, VA 24061

The estimation of cockroach population numbers is a continuing problem. Mark and recapture techniques have met with variable success. In this study, a removal method estimation was used in preparation for a sterile-male experiment on two Navy ships. The objectives were (1) to document reduction of population numbers prior to releases by estimating pre- and post-removal population size and (2) to make inferences concerning population age structures.

In cooperation with Navy entomologists, collections were made on 2 ships, one 62.5 m and the other 159.2 m in length. A synergized aerosol pyrethrin spray was used to flush cockroaches from harborage. Known or suspected harborage were then sprayed with 1% baygon in oil. All cockroaches appearing within 15 minutes of cessation of spraying were collected with a vacuum cleaner.

Two captures brought the population of the smaller ship to manageable levels. Capture probability was $.6851 \pm .0063$. Pre- and post-removal numbers were calculated with ca. 9% coefficient of variation. The large ship required 4 collections. Capture probability was lower ($.5077 \pm .0021$), as was the coefficient of variation (ca. 5%). All captures contained a preponderance of adults. Treatment caused a shift in the sex ratio toward a majority of adult females. Nymphal populations showed a 1:1 sex ratio. Male nymphs appeared to have 5 instars while females had six.

Assessment of insect damage to vegetation by remote sensing. V. Klemas, Univ. of Delaware, Newark, DE 19711

Insects cannot be detected directly from satellites or aircraft. However, changes in the spectral reflectance of plants can be used to assess insect damage to vegetation over large wooded and agricultural areas. Examples of successful remote sensing of insect damage include gypsy moth (*Porthetria dispar* (L.)) defoliation of mixed woodlands, citrus blackfly (*Aleurocanthus woglumi*) infestations in citrus groves, bark-beetle impacted conifers, and various crop diseases. Remote sensing techniques can significantly enhance the capability of ground-survey teams to assess insect damage because remote sensors map large areas at relatively low cost; use infrared

wavelengths which penetrate deeply into the leaf tissue to detect early loss of plant vigor; and employ multispectral analysis techniques which can detect smaller spectral reflectance changes than the human eye. While a limited amount of "ground truth" is still required, remote sensing techniques are being adopted by many groups and agencies as a cost-effective tool for assessing insect and disease damage to vegetation.

Loss assessments and decision-making for the tobacco budworm, *Heliothis virescens* (F.) (Lepidoptera:Noctuidae), on Maryland tobacco. D. M. Kolodny-Hirsch and F. P. Harrison, Dept. of Entomol., Univ. of Maryland, College Park, MD 20742

Despite the economic importance of tobacco, very little information concerning tobacco injury by the tobacco budworm is available. Therefore, during the growing season of 1977 field studies were conducted to investigate this pest on air-cured tobacco in southern Maryland. Specific objectives of our research were (1) to determine the damage-density relationships resulting from artificial infestations of the budworm at several growth stages of tobacco (2) to determine the theoretical economic-injury levels (EILs) of the budworm throughout several growth stages of tobacco. Percent yield and value reduction of tobacco was correlated with larval density at several growth stages of tobacco by multiple and linear regression procedures. Results of this study show that sensitivity to defoliation varies markedly with tobacco growth. Throughout most growth stages plants were able to compensate for some degree of foliar loss. Compensation was highest during growth periods showing rapid meristematic activity. Sensitivity was most evident during root formation and production of floral parts, although markedly less during the latter. Based on the above data, EILs for the budworm were determined by integrating several economic parameters with value-density relationships. EILs indicated that throughout most developmental stages of Md. 609 tobacco, large populations of budworms can be tolerated without sufficient damage to warrant suppression. Average EILs of 25% approach optimal benefit-cost relations.

Effect of habitat characteristics on the succession of outlet-breeding black flies (Diptera:Simuliidae) in New Hampshire. D. J. Lake and J. F. Burger, Dept. of Entomol., Univ. of New Hampshire, Durham, NH 03824

Hatching patterns, adult emergence sequence and temporal succession of outlet-breeding black flies, including habitat selection in sympatric sibling species of *Simulium venustum* and *S. verecundum*, were studied in N.H. Larval populations were sampled weekly at 5 pond outlet sites in a 10 km

radius around Waterville Valley. Habitat characteristics were determined by measuring the hydrological parameters, including pH, conductivity, dissolved gases, temperature, principal ions, benthic substrates and current velocities. Seventeen species were collected at study sites in 1978-79, 6 were isomorphic sibling species of *S. venustum/verecundum*. *S. venustum* sibling species begin hatching from late March to mid-May. The CC sibling hatches first, followed by A/C, AC (gB) and CC₂. All siblings appear to be univoltine except CC, which persists at some sites until late July. Both *verecundum* (ACD and A/C) species hatch from mid-May to mid-June, depending on water temperature at specific sites. Hatching of other outlet-breeding species after mid-May occurred simultaneously at several sites and was strongly correlated with water temperature. Adult emergence closely paralleled hatching sequence in all species. Succession patterns were strongly dependent on rate of increase in water temperature. Differences in hydrological parameters between sites were too small to explain differences in species occurrence at the study sites.

Computer-assisted instruction for pest management: ORCHARD and ALFWEEV. P. A. Logan, Univ. of Rhode Island, Kingston, RI 02881

Two interactive computer programs were written to help students learn to manage pests in dynamic agro-ecosystems. ORCHARD, written at Michigan State Univ. in 1977, considers principles of managing apple mites. Its 3 levels of difficulty require a student to 1) become familiar with simple predator-prey population dynamics (Lotka-Volterra), 2) to be aware of how changes in either the predator or the pest populations can affect the overall population stability, and 3) to make a profit in an orchard through an integrated program using predatory mites and contemporary miticides. ALFWEEV, originating at Michigan State and completed at the Univ. of Rhode Island in 1978, is a computer simulation of an alfalfa field and some of the insects found there, including alfalfa weevil (primary pest), aphids (secondary pest), weevil larval parasitoids and honey bees (non-target beneficials). Students manage pests and optimize yield (both quantity and quality of hay) by making critical day-to-day decisions on cutting or spraying strategy. Realistic weather forecasts, dynamic plant growth processes (changes in height, biomass, protein, fiber, and digestible nutrients), legal restrictions, etc. add to the game environment. Both programs are fully tested and are standardized to be easily adaptable to any computer. Both are supplemented with student guides and programmer manuals. ALFWEEV also has a separate teacher guide.

Predicting the impact of Colorado potato beetle (*Leptinotarsa decemlineata* Say) on yield. P. A. Logan and R. A. Casagrande, Univ. of Rhode Island, Kingston, RI 02881

The economic significance of CPB density as it changes in time has never been accurately quantified. We have developed an expedient dynamic predictor of CPB impact on early maturing potato varieties to serve until a more accurate multidimensional simulation can be built. To do this, we established a gradient of densities as follows: All adults in each of several 4×4 m plots were collected twice weekly and redistributed at 3, 1, 0.5, 0.1, and 0.05 times $1 \times$ lot density, taking advantage of the CPB's relatively sedentary behavior. Twice weekly, for 8–10 weeks, 30 counts per plot were made of egg masses per stem and larvae per stem. Of several alternatives, 3rd order exponential models (over degree-day base 10, adjusted for crop emergence date) fit these count data best. Comparison of plot yield with area under the incidence curve provided a useful, linear yield estimator. Finally, we developed a generalized incidence curve algorithm, capable of density-dependent shaping adjustment, suitable for projecting a first generation larval incidence curve (and subsequent yield loss estimate) from 1 or more early season larval samples.

Treatment of a nuclear polyhedrosis virus of *Autographa californica* Speyer with 5-Bromodeoxyuridine and determination of changes in virulence in four lepidopteran hosts. J. T. McClintock and C. F. Reichelderfer, Univ. of Maryland, College Park, MD 20742

The use of chemical mutagens to produce mutations in vertebrate viruses has been reported by several investigators. Chemical mutagenesis might provide a mechanism to increase virulence in insect pathogens, and ultimately enhance their potential for utilization in an integrated pest management program. The purpose of this study was to treat an insect virus that displays a relatively high degree of virulence for one insect and assess changes in virulence for several alternate hosts. Increased virulence with insect viruses has been achieved by serial passage and one published report exists concerning treatment with chemical mutagens which suggests that virulence might be under polygenic control.

This presentation concerns the effect of treatment of a nuclear polyhedrosis virus of *Autographa californica*, the alfalfa looper, with the chemical mutagen 5-Bromodeoxyuridine. Treatment was initially carried out in *Trichoplusia ni*, the cabbage looper, and the effect of treatment assessed in this host along with subsequent effects on virulence in *Heliothis virescens*, the tobacco budworm; *Heliothis zea*, the corn earworm; and *Spodoptera frugiperda*, the fall armyworm.

The consequences of using alternate hosts as a starting point for treatment with mutagens was found to be significantly important, as well as the overall effects of treatment on the LC_{50} and LT_{50} .

Consequences of host phenology for exotic scale insects. M. S. McClure, Connecticut Agric. Exp. Stn., New Haven, CT 06504

Two armored scales, *Fiorinia externa* Ferris and *Tsugaspidotus tsugae* (Marlatt) (Homoptera: Diaspididae), native to Japan coexist on Eastern hemlock and on numerous other native and exotic conifers in Connecticut. Studies were conducted from 1976–1979 to examine the phenological relationships between these exotic scales and their hosts and related effects on scale success. Differences in the phenology of 14 host species and related differences in concentrations of nitrogen and water in the newest foliage in June during peak colonization by nymphs resulted in differential scale success. Nymphs which colonized hosts whose foliage was relatively immature and contained high concentrations of nitrogen and water suffered less mortality, developed faster, and ultimately laid more eggs than nymphs which colonized hosts with relatively mature foliage containing low concentrations of nitrogen and water. The phenological relationships between Eastern hemlock and its exotic scales favored the success of *F. externa* whose nymphs colonized 2 weeks earlier than nymphs of *T. tsugae*. Greenhouse experiments demonstrated that earlier colonization by *F. externa* had adverse effects on *T. tsugae* success by reducing the amount of foliar nitrogen available to *T. tsugae* nymphs and by causing a greater portion of them to colonize older, low nitrogen foliage where fewer survived. At 18 of 20 sites where these scales coexisted on hemlock during 1976, *F. externa* demonstrated superior competitive ability during three years by excluding *T. tsugae* (14 sites) or by significantly reducing its population densities. The competitive superiority of *F. externa* is likely due to its greater compatibility with hemlock phenology.

Effect of *Agromyza frontella* Randani (Diptera: Agromyzidae) on alfalfa quality and yield. G. B. MacCollom, G. Baumann and J. G. Welch, Vt. Agric. Exp. Stn., Univ. of Vt., Burlington, VT 05405

The alfalfa blotch leafminer, *Agromyza frontella*, a newly introduced alfalfa insect, was first reported in the northeast U.S. during 1968. Conflicting views on economic damage to alfalfa have in some states resulted in chemical control recommendations. Five years of field experimentation on the control of the alfalfa blotch leafminer, and its subsequent effect on yield and quality have shown no benefit from insecticidal treatment. Quality as measured by amounts of protein and percentage digestibility showed no

significant differences between carbofuran and Pydrin treated plots having less than 1 mine/stem and control plots having over 30 mines/stem. No differences in yield as measured by dry weight were detected between the treated and untreated plots. Hand-separated leaflets, into blotched and unblotched samples from 1st cut alfalfa, showed no significant difference in crude protein. The average weight of a blotched leaflet was 0.9 mg less than an unblotched, indicating that one might expect yield differences, but this was not reflected in 5 years of evaluation. It is suggested that the alfalfa plant may compensate for the mining activity by putting out more leaflets, but this aspect has not yet been investigated. On the basis of these studies, the alfalfa blotch leafminer is not considered a serious alfalfa pest in Vermont, and as a result growers are advised not to initiate insecticidal treatment.

Effect of pirimicarb on natural enemies of *Myzus persicae* (Sulzer) (Homoptera: Aphididae). T. P. Mack and Z. Smilowitz, Pesticide Res. Lab., Dept. of Entomol., Pennsylvania State Univ., University Park, PA 16802

The effects of pirimicarb on the predaceous natural enemies of *M. persicae*, the green peach aphid (GPA) were determined in a potato (*Solanum tuberosum* L. var Katahdin) field as a step in the development of an integrated pest management system for the GPA on tablestock potatoes. These effects were determined by visually counting predators occurring on 24 randomly selected potato stems on several prespray and 4 postspray (20, 41, 116 and 164 hr) sample dates. The plots were treated with encapsulated methyl parathion 18 days prior to the test to facilitate GPA population growth and thus attract natural enemies. Pirimicarb was applied at 4 oz active ingredient/acre.

Coccinellid larval populations in treated and untreated plots were similar, with population peaks occurring 20, 41 and 116 hr postspray. Coccinellid pupal populations in both treatments were similar until 41 hr postspray, when the untreated population exponentially increased at a much faster rate than the treated population. *Hippodamia convergens* Guerin (Coleoptera:Coccinellidae) adult populations in treated and untreated plots were markedly different. The *H. convergens* adult population in the treated plot decreased exponentially until the end of the study, while the untreated population increased. *Coleomegilla maculata* (DeGeer) (Coleoptera:Coccinellidae) adult populations were also higher in untreated than treated plots. The adult *Coccinella transversoguttata richardsoni* Brown (Coleoptera:Coccinellidae) populations were variable in both treatments, with different peaks.

Development of adult abdomen in *Drosophila melanogaster* Meigen (Diptera: Drosophilidae). M. M. Madhavan and K. Madhavan, Biol. Dept., Holy Cross College, Worcester, MA 01610

The cell lineage of the histoblasts during metamorphosis of *Drosophila* has been studied by histological methods. The development of adult abdomen is characterized by three morphogenetic processes. (1) Mitosis and consequent increase in the number of cells in the histoblast nests. This mitotic activity parallels the increase in the titre of ecdysone. (2) Programmed cell death among the larval epidermal cells and the coordinated spreading of the histoblasts to their final positions replacing the epidermal cells. By 24 hr after pupariation, fusion of the anterior and posterior dorsal nests and that of ventral nest with spiracular anlage is complete. The dorsal nest fuses with the spiracular anlage by 28 hr and by 36–40 hr after pupariation the histoblasts have completely covered the abdomen. From the pattern of cell death, and spreading of histoblasts it is concluded that the larval cells provide a cue for the advancing histoblasts to what extent they can spread in the formation of the definitive segment border. (3) Differentiation of the imaginal epidermal cells resulting in the secretion of the cuticle and cuticular outgrowths characteristic of adult abdomen. The anterior dorsal histoblast nest gives rise to the region of the tergite bearing cuticular outgrowths, the posterior dorsal nest, possibly, to the intersegmental membrane and to the acrotergite of the following segment, the spiracular nest to the spiracle and the area surrounding it, and the ventral nest to the sternum and the pleura of the corresponding hemisegment.

Feeding behavior of Tabanidae (Diptera) on livestock. L. A. Magnarelli, Conn. Agric. Exp. Stn., New Haven, CT 06504

The feeding behavior of *Chrysops*, *Tabanus*, and *Hybomitra* species was observed to determine preferences in feeding sites on dairy cattle and patterns of blood ingestion. Females of 7 *Chrysops* species fed more frequently from the head areas than any other body region, whereas those of 4 *Tabanus* and 4 *Hybomitra* species commonly chose the sides, belly region, or legs. *Tabanus lineola* and *Tabanus quiquevittatus* fed avidly from the legs, and because of their abundance, these insects were of particular annoyance to livestock in pastures. Deer flies typically fed to repletion after initial feeding attempts, while horse flies (which attempted to feed from the sides and legs of animals) were frequently interrupted by host body movements and, consequently, had to pierce their mouthparts repeatedly into the animal's skin before they imbibed blood. It was not uncommon to observe *H. lasiophthalma* and *Tabanus atratus* females flying from one animal to another after unsuccessful feeding attempts. Internal examinations of host-seeking horse

flies, captured in pastures by dry-ice baited canopy traps, revealed small amounts of fresh blood in midguts and only partially developed (Stage II) ovarian follicles. Capillary precipitin tests sometimes detected mixed blood from bovines and equines. Feeding success (acquisition of full blood meals) varies with the insect species, site chosen for blood ingestion, and host response to biting individuals. Repetitive feeding attempts by tabanids on different host animals reinforce the importance of these insects as potential vectors of certain pathogens by mechanical transmission.

New approaches for screening passenger baggage at U.S. international airports. J. H. Mahaney, USDA, APHIS, PPQ, Hyattsville, MD 20782

Deregulation of airlines, increasing number of wide-bodied aircraft and low fares have caused a crisis at American international airports. Since 1960 air traffic has increased nearly 600%. Federal inspectional forces at airports have increased by only 100%. Further staffing increases are not likely. Inadequate airport facilities along with inadequate staffing have caused travelers to sit for over an hr in aircraft parked outside of congested terminals. Government review agencies believe there are too many Customs inspectors at airports and that baggage spot checks would suffice. Due to intense pressure from Congress, airlines and traveling public, Customs has devised inspectional systems to expedite travelers. Newer systems as Citizen By-Pass and One Stop require only 90 seconds processing. There is even a goal of 60 seconds. As passenger traffic increases (2 million additional seats will be available for the European run this summer and there is a projection of 25% increase of travel) it is felt that restrictions will be made on Customs inspections at certain saturated airports. Recommendations may be made for "spot checks" or for the European honor system called "Red door-green door" whereby the traveler decides whether or not to go through Customs. Any such departures from present inspectional systems could be most dangerous and extremely destructive to American agriculture which is valued annually at nearly \$500 billion.

Mate-seeking strategies in male flower flies (Diptera: Syrphidae). C. T. Maier, Dept. of Entomol., Conn. Agric. Exp. Stn., New Haven, CT 06504

Although male syrphid flies exhibit many different types of mate-seeking behavior, most search only near flowers and other resources utilized by females. I observed the mate-seeking behavior of males of more than 40 species in the subfamily Milesiinae and extensively studied that of *Mallota posticata* (Fabr.) and *Somula decora* Macq. in a sandy area in Illinois. Males of both *M. posticata* and *S. decora* utilized two different site-depen-

dent searching strategies. In the morning, they patrolled flowering plants at the forest edge and in a nearby field to find feeding females. In the afternoon, they waited near treeholes, potential egg-laying sites, to intercept females arriving to oviposit. Both mate-seeking areas were aggressively defended against conspecific and some nonconspecific intruders. Resident males of *M. posticata* won 95% of the encounters with conspecific males entering their territories near treeholes. Active territorial defense (i.e. flying in response to intruders), probably the most energetically costly activity performed by males near treeholes, accounted for only 2.4% and 2.9% of the total activity budget of *M. posticata* and *S. decora*, respectively. The mating success of males at each resource is probably related to the abundance of males and females and to the degree of sperm precedence.

A comparison of laboratory-reared and wild type gypsy moth *Lymantria dispar* (L.) males (Lepidoptera: Lymantriidae) V. C. Mastro, Gypsy Moth Methods Development Center, APHIS, PPQ, USDA, Otis AFB, MA 02542

Studies carried out between 1957 and 1973 explored the effects of gamma irradiation and chemical sterilants on male gypsy moth sterility. These and other studies indicated that laboratory reared insects were inferior to wild type males. Recent improvements in laboratory culturing of the gypsy moth have made possible the mass culturing of insects for sterile male release and virus production. However, little was known about the "quality" of insects produced. The experiments described summarize two years of comparison of wild type and laboratory-reared gypsy moths. Specifically these studies compared: the periodicities of eclosion dispersal and attraction to pheromone sources; the spacial distribution of dispersing males; the ability of males to locate natural and artificial pheromone sources; and the longevity of males in the field.

Results of these trials indicate that male gypsy moths reared in the laboratory for seventeen generations are competitive with several wild strains of males. Laboratory reared males are able to locate virgin females and (+) disparlure baited traps as well as feral males. In addition periodicities of the three activities monitored are similar. Furthermore, laboratory reared males were captured in nearly the same age classes as wild males. Dispersal patterns of the strains tested were not identical; but differences did not indicate that laboratory-reared males are at competitive disadvantage.

Seasonal dispersal of pitcher plant mites (Acarina: Anoetidae). T. N. Mather and E. P. Catts, Univ. of Delaware, Newark, DE 19711

The structure of the symbiotic community of aquatic arthropods associated with pitcher plants (*Sarracenia purpurea*) was studied from sites in

New Jersey and Delaware. Comparisons were made between these communities, and similarities and differences in species abundance and richness were noted. Anoetid mites, believed to be *Anoetus gibsoni*, were most abundant from New Jersey plants, but were found from Delaware plants as well. Little more than a species description is found in the literature concerning this mite. *A. gibsoni* commonly uses a non-feeding hypopal stage for dispersal from its overwintering site inside old pitcher plant leaves. Mites overwinter as hypopi, and dispersal of mites begins in the spring after new leaves are open. Techniques were investigated to determine mechanisms of mite dispersal to new leaves. Emergence traps placed over individual overwintering leaves were serviced twice weekly and freshly emerged insects were collected and examined for paratenic mites. Newly formed leaves were marked and collected at two day intervals, and their contents were examined for mite dispersants. Insect visitors were selectively blocked from entering newly opened leaves with screens of different mesh size. Parasagittal sections of leaves glued to glass were used to observe pitcher plant biota in situ.

Development of overwintered versus summer pupae of the alfalfa blotch leafminer *Agromyza frontella* Randani (Diptera: Agromyzidae). W. K. Mellors and R. G. Helgesen, Dept. of Entomol., Cornell University, Ithaca, NY 14853

The overwintered versus summer pupae of the alfalfa blotch leafminer (ABL), *Agromyza frontella*, differed consistently in their temperature-dependent developmental rates. Overwintered pupae developed about 25% faster than summer pupae. This difference was significant in attempts to computer simulate the timing of spring emergence of the ABL. The transition from summer to overwintered developmental rate characteristics in ABL pupae was analyzed by comparing simulations using each set of rates to observed adult emergence from field samples incubated at a constant 20°C temperature in the laboratory. In August, emergence was adequately simulated using the observed pupation dates and summer pupal rates. In November, emergence was adequately simulated using the overwintered pupal rates and assuming that the pupae were at the same stage of development after completion of a presumed period of diapause development. By November, the variation in developmental state among pupae in the field had decreased compared to the time interval during which these individuals had pupated in the late summer. These developmental differences have consequences in terms of both the ecology and management of the ABL.

A new Japanese beetle trap containing pheromone and floral lure as synergistic attractants. F. W. Michelotti and J. W. Seidenberger, J. T. Baker Chemical Company, Phillipsburg, NJ 08865

A simple, effective all-plastic Japanese beetle trap has been developed consisting of a set of interlocking vanes and an hourglass-shaped disposable plastic bag that is attached through four slits and hooks. A controlled-release Hercon™ strip containing minute quantities of Japanese beetle pheromone (R,Z-5-(1-decenyl)dihydro-2(3H)-furanone) is affixed to one of the vanes through an adhesive backing. A floral lure pack, containing a 69%/31% mixture of 2-phenethyl propionate and eugenol, respectively, is inserted through slots in the vanes. The trap is then suitably suspended by a hang-tie and the replaceable plastic bag can be conveniently disposed of when filled with beetles along with household refuse. Trap performance tests were carried out in Wooster, OH, during August 1978 in selected residential areas. The trapping devices caught large numbers of beetles (ca. 20,000) over a two-day period. Average catch per trap was over 1600 beetles. These catches were achieved without having to spray with chemicals. It was established that use of the natural sex attractant in combination with the floral lure, markedly increases the number of beetles caught when compared to captures using the floral lure alone.

Comparative effects of some insect growth regulators on development, morphogenesis, and reproduction of the female rice weevil, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae). J. Mkhize and A. P. Gupta, Dept. of Entomol. and Econ. Zool., Rutgers Univ., New Brunswick, NJ 08903

S. oryzae is an important stored products' pest throughout the world. Previous studies of the effects of insect growth regulators (IGRs) have shown that this insect pest is difficult to control, because it develops within the kernels. The objective of this study is to compare the effects of R-20458, Ro 20-3600, MV 678, methoprene and hydroprene on the developmental stages, morphogenesis, F₁ progeny, productivity index, percent reduction in adult emergence, oviposition, and egg hatchability of *S. oryzae*. These effects were studied in insects reared on IGR-treated wheat as well as in those treated topically. Both methods produced similar effects but at different dosages. All developmental stages are susceptible to the IGRs, the 4th larval and the pupal stages being the most susceptible. The number of larval-pupal and pupal-adult intermediates increased at higher dosages. Sclerotization was not uniform in pupal-adult intermediate, and in most the elytra and the hindwings were malformed. Internally, the ovarioles were attenuated. F₁ progeny decreased at higher dosages. Productivity index was lowest (2.06) and percent reduction in adult emergence highest (97.94) at a

topical dosage of 0.3 μ l of 30 ppm of R-2045 and Ro 20-3600, for example. None of the IGRs significantly affected oviposition and hatchability. A comparative account of the dosages used and their effects will be presented.

Effects of soybean plant populations and planting configurations on insect populations. J. W. Murphy and J. C. Smith, VPI and State Univ., Blacksburg, VA 24061

Essex variety soybeans were planted on July 5, 1978 in 12, 24 and 36-inch row spacings. Within each row spacing were populations of 1, 2 or 4 plants per square foot corresponding to 43,560, 87,120 and 174,240 plants per acre, respectively. In linear row foot comparisons, weekly shake cloth observations revealed that 36-inch row spacings had the highest numbers of the green cloverworm, *Plathypena scabra* (F.) and total numbers of phytophagous insects and predaceous insect totals. The 24- and 12-inch row spacings contained the second highest and least number of insects, respectively. There were no differences in the numbers of total phytophagous insects present in plant populations of 1, 2 or 4 plants per square foot. Significantly higher numbers of green cloverworms were found in plant populations of 4 and 2 plants per square foot compared to those found in populations of 1 plant per square foot. The greatest number of predaceous insects were found in plant populations of 4 and 2 plants per square foot though the numbers found in 2 plants per square foot were not significantly different from those found in populations of 1 plant per square foot. Generally, highest numbers of phytophagous insect totals, green cloverworms and predaceous insects were found in those planting configurations with the widest row spacings and densest plant populations within the rows. These results indicate a preference of insects in selection of soybean phytohabitat based on plant spacing.

Biological control of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westw.) (Homoptera: Aleyrodidae) by *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae). J. R. Nechols, Dept. of Entomol., Cornell Univ., Ithaca, NY 14853

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westw.) is a serious pest of many commercially-grown greenhouse crops. Control of this pest by conventional chemical methods is difficult for a number of reasons. Biological control by its parasite, *Encarsia formosa* Gahan, on the other hand, is a practical method for controlling the whitefly—both on short- as well as long-term crops. However, to use this natural enemy effectively, growers and extension agents need to know: (1) what greenhouse temperatures to maintain; (2) how many adult parasites to release (in relation to a

given host density); and (3) when these parasites should be released. From previous studies, both the optimal temperatures for the parasite (21–27°C), and the parasite:host release ratio (about 1:30) have been established. However, the problem of *when* to release adult parasites had not been well established. Therefore, I exposed each nymphal whitefly stage to *E. formosa* females. The results showed that both 3rd and 4th instar whiteflies are: (a) the most highly accepted stages by ovipositing *Encarsia* females, and (b) the most suitable stages for the parasite's development and survival. Thus, timing the release of *E. formosa* adults to coincide with these host stages results in efficient mass-rearing and successful colonization of the parasite. The application of this information to biological control trials on poinsettia and Clematis has contributed to the successful suppression of whitefly populations on these crops in commercial greenhouses.

Attack ecology of the sugar maple borer, *Glycobius speciosus* (Say) (Coleoptera: Cerambycidae). W. G. Newton, Dept. of Environ. and For. Biol., State Univ. of N.Y., Syracuse, NY 13210

This study was initiated to describe the status of sugar maples at the time of attack by the sugar maple borer, *Glycobius speciosus* (Say). A ten acre plot in a northern hardwood stand near Wanakena, NY, was chosen for examination. In 1978, all trees with evidence of sugar maple borer damage were felled. Uninfested stems were taken from the study plot as controls. Growth ring analysis was performed on three to five cross-sections from each tree. Parameters of the trees which were assessed for the time of attack include: growth rate, diameter at base, diameter at breast height, diameter at attack, height of attack, total height, aspect of attack, and aspect of scar. Trees were also described as they were at the time of study. Scars were aged, and this information was used to characterize the pattern of attack within the plot. Projections were made in order to describe the stand at each year during the infestation's history. The parameters of the trees from the time of attack were compared with the parameters at the time of study to illustrate the changes that take place after infestation. The most important factor describing trees prior to attack seems to be growth rate.

Biology of *Leptothrips mali* (Fitch) (Thysanoptera: Phlaeothripidae), a predator of orchard mites. M. P. Parrella and R. L. Horsburgh, Shenandoah Valley Res. Sta., VPI and State Univ., Steele's Tavern, VA 24476

A two-year sampling program in orchards on integrated pest control programs revealed that *Leptothrips mali* (Fitch) was one of the most abundant mite predators during 1977–78. A study of its biology was undertaken as part of an evaluation of this thrips' potential for inclusion in an integrated

mite control program. Laboratory rearing conditions were $23.9^{\circ} \pm 1^{\circ}\text{C}$, 14-hr photoperiod, and 80-100% RH. A total of 1521 eggs were removed from apple leaves; 92% were on the underside of the leaves along the midvein. The majority of eggs were laid singly; however, they were occasionally found in pairs. The duration ($\bar{x} \pm \text{S.D.}$ days) of the developmental stages were: egg— 7.9 ± 1.3 ($N = 145$), first instar— 6.0 ± 0.7 ($N = 34$), second instar— 6.3 ± 0.9 ($N = 18$), prepupa— 1.3 ± 0.4 ($N = 29$), pupa I— 1.7 ± 0.5 ($N = 19$), and pupa II— 4.0 ± 0.5 ($N = 27$). Total development time ($\bar{x} \pm \text{S.D.}$) from egg-adult was 27.0 ± 1.2 days ($N = 21$). Longevity of adult females ($\bar{x} \pm 5.0$ days) was 37.7 ± 25.9 and the total number of eggs oviposited per female ($\bar{x} \pm \text{S.D.}$) was 37.9 ± 30.4 . The presence or absence of males did not affect female longevity or fecundity. However, *L. mali* is arrhenotokous; unfertilized eggs become males. No direct feeding on apple leaves was observed and the thrips survived ($\bar{x} \pm \text{S.D.}$) for 2.8 ± 0.83 ($N = 16$) days on apple leaves alone. Normal development occurred on a strict diet of *Verbascum thapsis* pollen.

Quantification of *Myzus persicae* (Sulzer) (Homoptera:Aphididae) damage to potato foliage production. F. L. Petitt, Z. Smilowitz and E. S. Nolan, Pesticide Research Lab., Pennsylvania State Univ., University Park, PA 16802

The dynamic nature of plant growth processes necessitates that when assessing damage the developmental stage of the plant must be considered as well as the abundance of the pest. Five aldicarb levels were used in field plots to foster different green peach aphid, *Myzus persicae* (Sulzer), population densities. Plant foliage and tubers were harvested weekly during the growing season and wet and dry weights were recorded. Green peach aphids were sampled weekly in each aldicarb level. Foliage production models were developed for each treatment by regression of accumulated foliage dry weight on degree-days. These models were used to estimate foliage production for each treatment. Determination of the impact of pest density on foliage production for a specific time during the season was effected by regression of accumulated foliage dry weight on green peach aphid numbers. Quantification of the damage, resulting in a relative damage index, was accomplished by regression of the percentage foliage losses on green peach aphid numbers. The relative damage index, which was expressed as percentage foliage loss per green peach aphid, varied as the growing season progressed. The seasonal damage index was the relative damage index regressed on accumulated degree-days for foliage. Creation of the seasonal damage index facilitated examination of seasonal changes in the effects of aphid feeding on foliage dry weight accumulation. Early season infestations

resulted in greater percentage foliage reduction than did late season infestations in 1977.

Notal setae of first instar nymphs of five *Periplaneta* species (Dictyoptera: Blattidae). P. K. Powell, Dept. of Entomol., VPI and State Univ., Blacksburg, VA 24061

The cockroach species *Periplaneta americana*, *P. australasiae*, *P. brunnea*, *P. fuliginosa*, and *P. japonica* are all well known pests of man. However the morphology of the first instar nymphs of these species has not previously been well studied. Close observations of the pro-, meso-, and metanota with a scanning electron microscope at magnifications of 2000 \times and above revealed the presence of at least six types of setae. These can be divided into distinct groups on the basis of length, shape, and location. The types include 1) *long setae*, found on all five species and located primarily along the notal margins, 2) *moderately-long setae*, the most common setal type, found on all five species both along and within notal margins, 3) short setae, located along and within notal margins on all five species and the most dominant setal type on *P. americana* and *P. japonica*, 4) *proclinate setae*, which lie directly on the surface of the cuticle of *P. australasiae* and *P. fuliginosa*, 5) *chalazae*, located on the underside of the posterior margins of the nota of all five species, and 6) *small setae*, located on the postero-dorsal margins of the nota of *P. australasiae* and *P. fuliginosa*.

The chalazae and the proclinate setae are the most unusual. Owing to the position of the chalazae and their proximity to the next posterior segment, they probably function as mechanoreceptors. The proclinate setae lie directly on the surface of the cuticle. Their sockets seem to be sunken into the cuticle.

Mating behavior of the bee *Colletes thoracicus* (Hymenoptera: Colletidae). E. G. Rajotte and R. B. Roberts, Dept. of Entomol. and Econ. Zool., Rutgers Univ., New Brunswick, NJ 08903

A nesting aggregation of *Colletes thoracicus* was found in the sand traps of a golf course near Trenton, N.J. in May and June, 1979. Protandrous males fly 3–8 cm above the sand searching for females. Such males will land and briefly inspect any small dark object. An attractive female (probably virgin) emerging from the ground is covered by a tumbling mass of 5–15 males. Such males also attempt mating with each other. When one effects genital union with a female, other males disperse immediately. The copulatory pair then flies in tandem to nearby trees or shrubs to complete mating. One pair remained *in copula* for approximately 3.5 minutes. The male clasps the dorsum of the female abdomen. Both face the same direction. Attractive

females seem to release a sex pheromone that excites males. Males attempt copulation with freshly killed attractive females. The severed abdomen of a female seems at least as attractive as the head and thorax. Males were also attracted to the nozzle of a syringe that expelled air from a container filled with attractive females. Males attracted to the nozzle attempt to copulate with each other. In a previous study males have been observed to dig into the sand a few seconds before an emerging female had breached the surface. Behavior of these bees suggests the presence of a female sex pheromone. The rapidity with which the unsuccessful males lose interest in a copulating female suggests the presence of a pheromone which negates the effects of a female sex pheromone.

Interactions among willow herbivores as a determinant of feeding and ovipositional patterns of the imported willow leaf beetle, *Plagiodera versicolora* Laich. (Coleoptera:Chrysomelidae). M. J. Raupp and R. F. Denno, Dept. of Entomol., Univ. of Maryland, College Park, MD 20742

Current plant-herbivore theory suggests that young compared with mature foliage of long-lived plants, such as trees, is preferred by specialist herbivores. Analyses of leaves of the weeping willow, *Salix babylonica*, indicate that young leaves are less physically tough and have greater moisture and nitrogen content compared with mature leaves. Thus, young leaves appear to be a better resource than mature ones. Comparisons of the feeding behaviors of adults and larvae of *Plagiodera versicolora* indicate that adults preferentially feed on young leaves but larvae show no significant preference for either young or old leaves. While older leaves may be less nutritious, the survivorship of eggs and feeding success of young larvae may be greater on mature compared to young leaves. This was confirmed when willow leaves of different ages were surveyed and young leaves were found to be missing more often or more severely damaged by adult beetles and other herbivorous insects. Consequently, eggs and/or larvae of *P. versicolora* are probably much more likely to be disturbed or destroyed on young compared to old leaves. If egg or juvenile mortality is greater on young leaves, then selection should favor oviposition on mature foliage. Laboratory and field surveys of female egg-laying patterns confirm this prediction. It appears that the cost of laying eggs on leaves of poor nutrient quality is outweighed by a gain in juvenile survivorship there.

Insects that deform black cherry. C. O. Rexrode, Northeastern Forest Exp. Stn., Delaware, OH 43015

Many black cherry, *Prunus serotina* Ehrh. seedlings and saplings have forked or crooked main stems. This results in pole stands with a high pro-

portion of deformed trees, and consequent reduced timber value. Results of a 2-year study of stem deformity in black cherry in Pennsylvania and West Virginia revealed that insects, diseases, forest, and browsing by deer were the major causes of injury to the terminal shoots of seedlings and saplings. Twenty-seven species of insects from 19 families and 5 orders were associated with young black cherry trees in six study areas. Of these species, *Archips* (Lepidoptera: Tortricida) accounted for up to 36 percent of the deformed stems and *Cecidomyia serotinae* O.S. (Diptera: Cecidomyiidae) accounted for 0 to 43 percent of the deformity. Reducing stem deformity in black cherry caused by these two species of insects is a complex problem because the degree of infestation varies from year to year. Although insect damage may be found in less than 20 percent of the trees in a plantation in any one year, the damage to shoots is compounded over a period of years. Also, the insects that cause the deformity have different habits and life cycles, which makes control difficult.

Sexual behavior in Hawaiian *Drosophila* (Diptera: Drosophilidae). J. M. Ringo, Univ. of Maine, Orono, ME 04469

Endemic Hawaiian species of *Drosophila* are distinguished by their diverse and spectacular morphology and mating behavior, and by their extraordinary rates of speciation. Many, perhaps hundreds, of these species have a dramatic sexual habit: mating at lek or arenas, a sexual habit once thought to be confined to birds.

The frequencies and sequencing of sexual displays in *D. grimshawi*, a "model" Hawaiian species, and in two closely related, morphologically similar species have been measured and found quite distinct. Individuals of these species can be separated with little error by discriminant functions.

The frequencies of some male displays in *D. grimshawi* are density-dependent. Increasing density causes courtship to increase. When females are present the ratio of contact to noncontact aggression increases linearly with density (fighting becomes more "intense"). The frequency of communal displays and aggression are positively correlated only when females are present, supporting the idea that the tendencies to disperse are balanced in a lek. These experiments show that whereas males initiate courtship towards male and female conspecifics at random, they respond to the presence of females in some of their other sexual behavior (aggression and communal displays).

The sequential organization of male sexual behavior is nonrandom but loosely organized. Information theoretical analysis shows differences between this behavior and the courtship rituals of continental *Drosophila* and other insect species.

Oviposition behaviour and egg distribution of the European apple sawfly *Hoplocampa testudinea* Klug. (Hymenoptera:Tenthredinidae). B. D. Roitberg and R. J. Prokopy, Univ. of Mass., Amherst, MA 01003

When presented with apple blossoms in laboratory cages, 15 of 18 (83%) female sawflies visited previously searched blossoms and 15 of 16 (94%) unsearched blossoms. Following feeding on pollen and nectar, females crawled to the receptacle where they displayed little (duration $\bar{x} = 5.7s \pm SE1.2$, $N = 14$) overt searching behaviour. Females pierced the receptacle with their ovipositors and deposited a single egg (duration of successful oviposition $\bar{x} = 121.0s \pm SE9.9$, $N = 13$). Following oviposition attempts which exceeded 45s, females fed on exudate from the oviposition puncture. Of females which visited previously unsearched blossoms, 16 of 19 (84%) attempted oviposition. Of females which visited blossoms which had just received an oviposition, 18 of 23 (77%) attempted oviposition. These data strongly suggest that, unlike another apple pest, *Rhagoletis pomonella*, female sawflies do not deposit an oviposition deterring substance. Sawfly larval infestations were normally distributed among the fruit of three sampled apple trees ($N = 208$ infestations in 838 fruit examined.) Selection pressure for development of an oviposition deterring substance in this sawfly may be weak because (1) there is normally a profusion of host blossoms, (2) larvae are mobile and move between fruits in a cluster, and (3) sawflies usually (87% of 110 cases examined) deposit an egg in only 1 or 2 of the ca. 4–5 blossoms per cluster, thus leaving the other 2–4 fruits for subsequent exploitation by larvae.

Anomalous oviposition behavior by the gypsy moth (Lepidoptera: Lymantriidae). M. C. Rossiter, State Univ. of New York, Stony Brook, NY 11794

Choice of oviposition site has been correlated with subsequent larval fitness. Previous research on the gypsy moth, *Porthetria dispar*, indicates that the female oviposits on the tree which serves as the food source (except under conditions of very high density). Because the female moth does not fly, her choice of pupation site becomes her oviposition site.

This study of oviposition preference was done in oak-pitch pine woodlands in New York, New Jersey, Pennsylvania and Massachusetts. Study sites contained gypsy moth populations with densities ranging from low to high. Oak, the predominant tree in all localities, is considered to be the most preferred food in the northeastern U.S. Trees were sampled along a transect and were scored according to tree type and presence or absence of egg masses. Analysis of the data showed that preference for oviposition on pitch pine was significant for all localities except New Jersey.

Pitch pine is not a suitable food for early larval development as instars I–

III cannot or will not eat the needles, yet females prefer pitch pine as an oviposition site. During the first 48 hr after hatch, the larvae will disperse, a passive ballooning process dependent upon the wind, if appropriate food is not encountered or if conditions are crowded. Thus, hatchlings oviposited on pitch pine must disperse to avoid starvation. This data provides a foundation for further study on the advantages and disadvantages resulting from preferential use of pitch pine as an oviposition site.

Adaptations of the fall cankerworm *Alsophila pometaria* (Harris) (Lepidoptera: Geometridae) to unapparency of host leaf flush. J. C. Schneider, Princeton Univ., Princeton, NJ 08540

The fall cankerworm is subject to selection to increase synchrony of time of egg hatch with host foliation. I have asked the question of how the fall cankerworm has reacted evolutionarily to variation in time of host foliation on two spatial scales: 1) within stand—among individual trees (1 m) and 2) among stand—among species of hosts (100 m). Hatchlings can survive for only about three days without food. Late hatch by a few days on red maple resulted in a 50% decline in potential fecundity. Red maple leaves toughen at an age of 28 ± 2 days. Thus the larval stage must coincide with an approximately 30-day long window. Individual trees tend to foliate consistently early or late. The average weight of prepupae dropping out of a given tree is positively correlated with the average weight of the apterous females climbing the tree the next fall. Thus female aptery results in oviposition on the same tree on which the female fed as a larva and presumably increases synchrony of hatch with foliation. The average date of foliation of black oaks can be six days later than that of red maples. The egg masses in a stand of black oak hatched three days later on average than those in a stand of red maple 150 m away. This is due to differences in the hatching characteristics and times of oviposition of the clones specializing on the two species. Thus differences in hatching time of host races match differences in host species' average times of foliation.

Delayed hatching of Japanese wax scale *Ceroplastes ceriferus* (F.) (Homoptera: Coccidae) in locations strongly affected by marine winds. P. B. Schultz, Virginia Truck and Ornamentals Res. Stn., Virginia Beach, VA 23455

The Japanese wax scale, *Ceroplastes ceriferus* is generally distributed throughout the southeastern states. It attacks a wide variety of ornamental plants and is very prolific. The scale overwinters as an adult female and oviposition begins in eastern Virginia in early May. Scale populations on *Ilex cornuta* var. *bufordii* at five sites in the Norfolk metropolitan area were examined weekly beginning June 12, 1978 and the percentage of hatched

eggs was determined weekly at each site. All weather stations in the study area provided daily maximum and minimum temperatures which were compared to the hatching rate.

On June 12, 1978 the hatching at the southern exposure of the most urban location was 80%, while hatching had not begun at locations near Chesapeake Bay or the Atlantic Ocean. One week later all sites, except near the Atlantic Ocean, had hatching percentages of 70% or higher; only 15% were hatched at Cape Henry along the ocean. The delay in hatching of the wax scale at Cape Henry is attributed to the strong eastern airflow along the coastline that results in lower maximum temperatures in spring months. In the urban location the buildings protect the scale-infested plants from the marine breezes and produce the heat-island effect, with reduced evening cooling due to reradiation.

Application of pheromone technology in the gypsy moth program. C. P. Schwalbe and E. C. Paszek, USDA, PPQ, Otis Methods Development Center, Otis AB, MA 02542

The optically active (+) enantiomer of disparlure is a potent attractant of male gypsy moths. Traps baited with this material are effective devices for determining the occurrence and distribution of this pest. A series of field tests was conducted to define probabilities of capture of moths within various arrays of traps and to describe adult dispersal behavior in areas trapped. As trap density decreases, the probability of capturing moths declines. Trap arrays with intertrap distances (ITD) of 800 m recover ca. 1% of the released population; 22% was recovered when traps within the array were spaced 175 m apart. It appears that dispersal behavior of males is similar in trapped and untrapped areas. A grid of traps (ITD = 175 m) established on an area where moths had been released 48 hr earlier. The distribution of captured insects was similar to that found when moths were released into the trap grid. Most insects (ca. 70%) were captured in traps 275 m from the release point. These data were used to develop a system for estimating probable boundaries of infestations based upon adult distribution.

The techniques have been applied in two pilot tests in natural infestations. Both surveys yielded capture patterns which indicated the centers of the infestations. In one test area, ca. 9 sq. mi. had been presumed to be infested (based upon earlier surveys). Using the new techniques, it was found that only ca. 1 sq. mi. was actually infested, thus minimizing the area to be subsequently involved in control efforts.

Life history strategies of spring feeding forest Lepidoptera. D. F. Schweitzer, Peabody Museum, Yale Univ. New Haven, CT 06520

Data obtained from outdoor observations in CT, primarily with the noctuid tribe Lithophanini, indicate that overwintering as non-diapausing eggs results in very early, highly staggered hatching. Early spring oviposition results in similarly staggered, but later, hatching commencing near the time of spring foliation. A winter egg diapause usually results in synchronous hatching shortly after foliation of the host. However, some *Catocala* have staggered hatching despite such a diapause. Spring ovipositing Lithophanini attained closer synchrony (measured in degree-days base 5°C) of egg hatching with foliation in 1975 and 1978, years with rather cool, late springs, than in 1976 and 1977, when temperatures over 30°C caused early foliation. Such adjustable synchrony apparently reduces the risk from unfavorable weather which is especially likely to follow an early foliation, but results in less favorable food quality. Staggered hatching dates appear to maximize minimum larval fitness in an environment characterized by erratic weather and unpredictable foliation dates.

Effect of planting date on the abundance of insect pests on flue-cured tobacco. P. J. Semtner and T. R. Terrill, Southern Piedmont Res. and Continuing Education Center, Blackstone, VA 23824

Research was conducted to determine the effect of planting date on the occurrence of tobacco hornworms, *Manduca sexta* (Linnaeus) (Lepidoptera: Spingidae), tobacco budworms, *Heliothis virescens* (Fabricius) (Lepidoptera: Noctuidae), and tobacco flea beetles, *Epitrix hirtipennis* (Melsheimer) (Coleoptera: Chrysomelidae) on flue-cured tobacco. Tobacco was transplanted at 10-day intervals for 3 dates beginning May 6. The experiment was established in a split-split plot design replicated 3 times.

At 2 wk after the last transplanting, tobacco flea beetles caused significantly ($P < 0.05$) more damage to tobacco transplanted on the middle date than on tobacco transplanted early or late. During 1977, the late planted tobacco had significantly fewer flea beetle feeding holes than the early or medium planted tobacco. The smaller leaf size of the late tobacco and a decline in flea beetle populations during late May and early June were responsible for reduced tobacco flea beetle feeding. When compared to early and medium planted tobacco, flea beetle populations were significantly lower on late tobacco during June. However, during August the late tobacco had the highest flea beetle populations.

Tobacco budworms were most prevalent ($P < 0.01$) on early planted tobacco, averaging $3\frac{1}{2}$ times more budworms/acre than tobacco planted 10 days later and 8 times more budworms than tobacco planted 20 days later. Tobacco hornworms were most abundant on late planted tobacco.

EDNH-stimulated ecdysone production by ovaries of *Aedes aegypti* (L.) (Diptera: Culicidae). J. P. Shapiro and H. H. Hagedorn, Dept. of Entomol., Cornell Univ., Ithaca, NY 14853

In vitro evidence supports the hypothesis that the egg development neurosecretory hormone (EDNH) of the yellow fever mosquito, *Aedes aegypti*, acts by stimulating ecdysone synthesis and secretion by the ovary. Ecdysone may subsequently stimulate vitellogenin synthesis by the fat body. We studied specific aspects of the ovarian response to EDNH *in vitro*.

Incubations of ovaries with mid-brain of adult females stimulate ecdysone secretion into medium. Ovaries and incubation medium contain negligible amounts of ecdysone prior to incubation, as determined by radioimmunoassay (RIA). Upon incubation of ovaries with a saline extract of heads, nanogram quantities of ecdysone appear in the medium, with little remaining in ovaries. Actual secretion *in vivo* is indicated by distribution of ecdysone in tissues from blood-fed animals.

Ecdysone secretion by ovaries upon exposure to EDNH extracted from whole heads occurs in a time-dependent manner, beginning within one hour and continuing at least 10 hours. Secretion is dose-responsive to whole head extract.

The ovary does not develop the capability to respond to head extract until 36 hours after eclosion; maximal responsiveness is reached by 60 hours at 27°C. Development of ovarian responsiveness to EDNH may be due to the influence of juvenile hormone during the first 36 hours after emergence.

Encapsulation of pollen attractants for honey bee, *Apis mellifera* L. diets (Hymenoptera: Apidae). E. W. Herbert, Jr., H. Shimanuki and B. S. Shasha, USDA, Beltsville, MD 20705

Honey bees usually prefer to collect fresh pollen when given a free choice between pollen and pollen substitutes. The addition of attractive fractions from pollen to increase consumption of bee diets was studied. Pollen substitutes containing whey and yeast as protein sources were supplemented with polymers (2, 4, 6 or 8% dry weight) produced by encapsulation of the chloroform fractions from fresh bee collected pollen in a starch matrix. Diets containing each level of starch-encapsulated lipid was fed to four colonies of caged bees and the rate of brood rearing and diet consumption was measured for 12 weeks. The bees fed whey-yeast diet containing starch encapsulated pollen lipids were able to rear significantly more brood to the sealed stage than bees fed the whey-yeast diets without attractants. Bees fed the diets containing either 2 or 4% encapsulated lipids reared 2½ times as much brood to the sealed stage as control bees. Bees fed both levels (2 and 4%) equalled the levels by bees fed pollen. Bees fed the poorest diet (containing 8% lipid) were able to rear twice as much brood as control bees. Consump-

tion by bees of all diets containing pollen extracts was significantly better than for bees fed the attractant free control. The addition of attractive fractions from pollen to substitute diets not only increased consumption of the diet but also eliminated the possibility of spreading chalkbrood disease, *Ascosphaera apis* by the addition of whole pollen to diets.

Establishing economic parameters for green peach aphid, *Myzus persicae* (Sulz.) (Homoptera: Aphididae) damage on commercial potatoes. Z. Smilowitz, M. E. Whalon, E. S. Nolan and C. A. Martinka. Pesticide Res. Lab., Dept. of Entomol., Pennsylvania State Univ., University Park, PA 16802

Following establishment of green peach aphid, *Myzus persicae* (Sulzer) (GPA), impact on potatoes the economic consequences of the damage must be assessed. The procedure used for GPA-CAST, a computerized pest management system for GPA on commercial potatoes incorporated a market model, management cost and pest damage index. Pest impact data were obtained from plant production models and pest densities. A matrix model was developed to estimate market values which generated 12 distinct crop values. The percent loss/GPA/leaf throughout the growing season, seasonal damage index (SDI), was interfaced with the market model to determine monetary losses. The monetary damage index (MDI), dollar loss/GPA/leaf, the monetary counterpart of SDI, was obtained as follows: $MDI = SDI/FT \times \text{crop value}$ ($FT = \text{foliage tuber ratio}$). Dynamic economic injury levels (EIL) were obtained from these values and insect management costs per acre. $EIL = \text{management cost}/MDI$. The economic threshold levels (ETL) were calculated from the EIL and the projected GPA population growth rate. The latter was based on the expected accumulated degree days ($^{\circ}D$) for GPA at a specific interval during the growing season. A 3–4 day period between recommendation and time of application permitted growers ample time to take appropriate action. The time period averaged out to be 100 accumulated $^{\circ}D$. Therefore, the ETL for any interval during the growing season became the EIL that occurred 100 accumulated $^{\circ}D$ prior to the current accumulated $^{\circ}D$ for GPA.

The bee louse, *Braula coeca* Nitzsch (Diptera: Braulidae), its distribution and preference for queen honey bees. I. B. Smith, Jr., and D. M. Caron, Maryland Dept. of Agric., Annapolis, MD, 21401 and Univ. of Maryland, College Park, MD 20742

A survey was conducted in Maryland to determine the infestation level of bee lice in honey bee colonies. 1881 colonies in 272 apiaries were examined during inspections by the Maryland Department of Agriculture. Bee lice were observed in 28% of the apiaries and 18% of the colonies. In apiaries with lice 50% of the colonies contained lice.

Four frame honey bee nucleus colonies were established and stocked with 50 *Braula coeca* each. One or more lice were present on 24% of the mated queen honey bees observed between August and December. Only 2% of the virgin queens observed harbored lice during the same period. Almost no lice were present on queens during preceding months. In an established apiary known to be infested with *Braula*, no lice were observed on queens April through June 15. 62% of the queens examined from June 16 through the rest of the season harbored lice and 58% of these lice were pale in color, indicating *Braula* were less than one-day old. It appears that newly emerged bee lice are attracted to mated queens.

Rearing of *Tabanus nigrovittatus* Macquart (Diptera: Tabanidae) from egg to adult. R. K. Sofield and E. J. Hansens, Dept. of Entomol. and Econ. Zool., Rutgers Univ., New Brunswick, NJ 08903

Host-seeking female salt marsh greenheads, *Tabanus nigrovittatus*, were collected from box traps on a salt marsh near Cedarville, NJ. Flies were allowed to blood feed on human forearm or restrained guinea pig. Ten egg masses were oviposited by these flies. The egg masses turned grey-brown with a chalky covering several hours after oviposition. The egg masses were loosely cemented together. Each egg mass was removed from the cage and placed on moist filter paper in a petri dish until hatching occurred. Seven masses hatched after 5 days yielding 508 larvae. Larvae were reared at 27 C in individual 8 dram vials with wet filter paper. Every 2–5 days the filter paper was changed and fresh food (house fly maggot or earth worm) provided. Larval mortality was highest in the first 40 days. Only 12.5% of the larvae survived this period. Three to five months after hatching, half the larvae were subjected to 5 C for 40 days and the remainder for 80 days. The rearing temperature was then returned to 27 C. Pupation of 26 larvae from four egg masses occurred 6–9 months after hatching. A single larva pupated 60 days after hatching. The pupal stage lasted 7–12 days. Of the 14 females reared, 7 oviposited a mass of infertile eggs, 3 took a blood meal after oviposition, and one fly oviposited a second mass of infertile eggs.

Transmission of equine babesiosis and bovine anaplasmosis by *Dermacentor albipictus* (Packard) (Acari: Ixodidae). D. Stiller, W. M. Frerichs, G. Leatch*, and K. L. Kuttler, Animal Parasitol. Inst., SEA, USDA, Beltsville, MD 20705, and *Commonwealth Sci. and Indust. Res. Org., Indooroopilly, QLD 4068, Australia

Although the 1-host winter tick, *Dermacentor albipictus*, is a common parasite of horses and cattle and is widely distributed in the U.S., its role as a potential vector of the hemoparasitic diseases equine babesiosis and bovine anaplasmosis has been little studied. Experiments to assess the vec-

tor competence of the inornate form of *D. albipictus* for the horse hemoparasite *Babesia caballi* revealed that (1) 70% of female ticks fed on an infected pony became infected, as demonstrated by Giemsa-stained smears of tick hemolymph; (2) the F_1 progeny of these females were infected transovarially and transmitted the infection when test-fed on susceptible ponies; and (3) male ticks transmitted the infection after being removed from an infected pony, held for 1 hr, and transferred to a susceptible pony. Similar experiments with this tick and the cattle hemoparasite *Anaplasma marginale* indicated that (1) nymphal ticks, fed as larvae on an infected calf, transmitted anaplasmosis when test-fed on a susceptible calf and (2) male ticks transmitted the infection after being removed from an infected calf, held for 1 or 4 hr, and transferred to susceptible calves. Tests of transovarial transmission are in progress. This is the first unequivocal evidence incriminating *D. albipictus* as an experimental vector of these pathogens and suggests that this tick may be a potential vector of these agents in nature.

Soybean foliage consumption by the adult Mexican bean beetle, *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae). I. M. Sunzenauer¹, T. Elden², and A. L. Steinhauer¹, Dept. of Entomol., Univ. of Maryland, College Park, MD 20782¹ and USDA, SEA, Beltsville, MD 20705²

Foliage feeding studies have been conducted on a variety of soybean insects, but are lacking for the adult Mexican bean beetle. Such information is needed by researchers developing decision-making models for the Mexican bean beetle in soybeans. In this study the daily feeding rate of the adult Mexican bean beetle was determined by measuring leaf area consumption. Daily oviposition rates were also obtained. Three different populations of adults were used. Population I consisted of 2nd generation adults, Population II consisted of adults which had overwintered in the field, and Population III consisted of adults which had overwintered in the laboratory. Pairs of beetles in each study were set up in petri dishes in an environmental chamber with fresh foliage, which was changed after specific time intervals, and the number of eggs was recorded. Consumed leaf area was measured by a LI-COR Leaf Area Meter from the Lambda Instruments Corporation. The mean daily leaf area consumption rates for Populations I, II, and III were 4.65 cm²/day, 4.87 cm²/day, and 3.80 cm²/day respectively. The mean daily oviposition rates for Populations I, II, and III were 11.10 eggs/day, 6.77 eggs/day and 5.37 eggs/day. The lower feeding and oviposition rates for Population III resulted in part from the 7 months in cold storage.

Humidity tolerances of 3 species of phytoseiid mites (Acarina: Phytoseiidae). F. C. Swift and L. Blaustein, Rutgers-The State Univ., New Brunswick, NJ 08903

The effects of humidity on hatching success, survival of adult females, and rates of feeding and oviposition were determined for *Neoseiulus fallacis* (Garman), *Neoseiulus mckenzei* (Schuster and Pritchard), and *Amblyseius andersoni* Chant. Each factor was measured at relative humidities of 43, 51, 64, 75, 85, 90, and 97%. All experiments were conducted at 25°C and a 16:8 light-dark cycle. Eggs of *A. andersoni* showed the greatest resistance to desiccation. Also, *A. andersoni* females deprived of food survived longer than either *N. fallacis* or *N. mckenzei* at lower humidities, but the latter species survived longest at the highest humidity. Survival time over the range of humidities was exponential for all 3 species. The feeding rate of *N. fallacis* was most affected by humidity, showing approximately a 3-fold increase from the highest to the lowest humidity. Oviposition rates of *N. fallacis* and *A. andersoni* were affected only slightly by humidity, but the oviposition rate of *N. mckenzei* declined rapidly at humidities below 75%. A ratio of oviposition rate/feeding rate was used as a measure of humidity niche breadth, using Levin's formula (1968), divided by the number of resource states. According to this formula, *A. andersoni* had the widest niche breadth (0.96), followed by *N. fallacis* (0.82) and *N. mckenzei* (0.50). However, *N. fallacis* compensated by certain behavioral adaptations; namely, higher feeding rates at lower humidities and the placement of eggs in microhabitats of higher humidity.

Hudson Porta-Pak ULV Sprayer. R. Treichler, H. D. Hudson Manufacturing Company, 500 North Michigan Ave., Chicago, IL 60611

The Hudson Porta-Pak Sprayer is the only back-carried motorized unit that is designed specifically for use in ultra-low-volume pesticide application. The air volume output at full throttle is 400 CFM; the air speed at the nozzle is 230 MPH. The pesticide tank holds 106 ozs; the fuel tank 68 ozs. With a nominal discharge rate of 1.6 ozs. p.m. a full tank supplies 1 hr of application or ½ hr at a full discharge rate. Walking at 1.1 MPH, over 1 mile will be covered discharging 1 tank full at 1.6 ozs. p.m. If the application is horizontal, the 50 foot swath and 1 pesticide tank contents will cover a 7½ acre area. Hudson Porta-Pak is ideal for fruit and ornamentals. Solutions, emulsions and suspensions of wettable powders can be used to apply pesticide to trees, shrubbery and truck crops. Porta-Pak is especially useful in cattle feed lots and swine confinement areas to control mosquitoes, flies and other pests. The turbulent air stream and spray swath of 40 ft. vertical and over 50 ft. horizontal makes it especially suited for both fruit and ornamental

trees. The Hudson Porta-Pak Sprayer is ideal for mosquito and fly control in parks, stadiums, playgrounds and picnic areas.

Integration of *Rhinocyllus conicus* Froelich larvae (Coleoptera: Curculionidae) and 2,4-D for control of *Carduus nutans* L. J. T. Trumble and L. T. Kok, Dept. of Entomol., VPI & State Univ., Blacksburg, VA 24061

Herbicidal effect on *Rhinocyllus conicus* Froel., a thistle head weevil, was studied by examining the mortality, emergence rates and weights of weevils developing from plants treated with 2,4-D (LVA). Infested heads, obtained by caging ovipositing *R. conicus* on primary heads of musk thistle (*Carduus nutans* L.), were treated with 2,4-D at 1.68 kg/ha 0 to 3 weeks after oviposition. Mortalities of larvae developing from untreated plants and those plants sprayed 1 to 3 weeks were significantly lower than mortality from plants sprayed within 48 hr of oviposition. The latter failed to support larval development beyond the second instar. Developmental times and weights of weevils that emerged from blooms sprayed at 1, 2, and 3 weeks were not significantly different from controls. Plants sprayed up to 2 weeks after oviposition (late-bud to early-bloom) did not produce viable seeds, but treatments at 3 weeks after oviposition (full-bloom) allowed 10% germination of seeds not damaged by *R. conicus* in primary heads, and plants survived to produce additional heads. Treatment of musk thistles with 2,4-D at late-bud to early-bloom stage of the primary heads prevented formation of viable seeds without adversely affecting *R. conicus* development.

Characterization of the structural components of the granulosis virus of *Plodia interpunctella* (Lepidoptera: Pyralidae). K. A. Tweeten, 2810 Fawkes Dr., Wilmington, DE 19808

Procedures were developed for isolation of the following structural components of *Plodia interpunctella* granulosis virus: granulin, enveloped nucleocapsids, nucleocapsids, capsids, and DNA. Biophysical and biochemical techniques were utilized to extensively characterize these components. Two molecular forms of DNA were extracted from the virus. Twenty-five percent of the DNA was isolated as covalently closed circles; the remaining seventy-five percent consisted of relaxed circular molecules. The molecular weight of the DNA was estimated to be 80×10^6 daltons from sedimentation in neutral or alkaline sucrose gradients and from electron micrographic length measurements. The polypeptide composition of each viral component was determined by sodium dodecyl sulfate discontinuous polyacrylamide slab gel electrophoresis. The enveloped nucleocapsids consisted of fifteen structural proteins ranging in molecular weight from 12,600 to 97,300. Of these proteins, eight were present in nucleocapsids. The major nucleocapsid

proteins had molecular weights of 12,500 (VP12) and 31,000 (VP31). Gel electrophoresis provided evidence that VP31 was the major capsid polypeptide while VP12 was an extremely basic protein which was located inside the capsid, probably in association with the viral DNA.

Biological characterization of AMBUSH insecticide. M. Tysowsky, ICI Americas, Biological Research Station, Goldsboro, NC 27530

AMBUSH, a synthetic pyrethroid insecticide being developed by ICI Americas has been used successfully under grower conditions over the past two years for control of Lepidoptera and a number of selected Coleoptera. Rates of 0.05–0.2 lb ai/A have been evaluated on pests which attack apples, celery cole crops, corn, cotton, lettuce, potatoes, tomatoes and soybeans. However, very little has been reported concerning the biological properties of this new chemical.

AMBUSH works by contact and it is extremely effective when ingested. The material acts as disruptant. Lab and field tests have demonstrated that although insects may not die quickly, feeding stops within minutes after contact. Death may take from 24–72 hours. AMBUSH provides a high level of activity against various instars of lepidopterous larvae with some control of adults and suppression of egg hatch. Bioassays with Lepidoptera have shown that this material possesses ovicidal activity comparable to that achieved by chlordimeform. Tank mixes with other insecticides are not recommended as they can result in delayed crop maturity.

The material is environmentally sound and has a wide margin of safety to humans. However, like the natural pyrethrins, it is toxic to bees and fish. AMBUSH is very stable under sunlight conditions and it is tightly bound to soil particles.

Gas-liquid chromatographic comparisons of the cuticular lipids from male and female house crickets, *Acheta domesticus* (L.) (Orthoptera: Gryllidae). E. C. Uebel and J. D. Warthen, Jr., Biol. Act. Nat. Prod. Lab., AEQI, USDA, SEA, Beltsville, MD 20705

The main objective in the investigation of the cuticular lipids of the cricket was to check for compounds that were more abundant on the adults of one sex than on the other and which might serve as recognition pheromones for members of the opposite sex. R. Paul (Nature, 1976. Vol. 263:404–405) has demonstrated that the males of several species of ground crickets are able to detect chemical stimuli from conspecific females and respond with calling songs. The hydrocarbons and cuticular lipids from mixed sexes of house crickets have been identified by Hutchins and Martin (Lipids. 1968. Vol. 3:250–255) and Blomquist et al. (Comp. Biochem. Physiol. 1976. Vol.

54B:381–386). Gas-liquid chromatography on 2% OV 101 showed both a qualitative and quantitative similarity between the cuticular lipids present on adult females, 8th-instar males, and 8th-instar female nymphs. However, the adult males produced much more material chromatographing between 36- and 37-carbon *n*-alkane standards. This large peak of material consisted of ca 13% saturated and 87% unsaturated hydrocarbon. Approximately 33% of the 37-carbon unsaturates were monoenes and 66% were dienes. At the present time we are trying to characterize these male 37-carbon mono- and dienes by locating the positions of the double bonds and the methyl branching. Whether these male-produced monoolefins and diolefins have a communicative function between the males and females or between other males remains to be investigated.

Life history and population dynamics of tree-dwelling Homoptera. J. W. Webb, Oak Ridge Nat. Lab., Oak Ridge, TN 37830

There are few instances in which the role of the host plant in the population dynamics of herbivorous insects has been assessed in the field. Two studies of leaf feeding Homoptera were undertaken to help elucidate this role. Estimates of field population numbers and biomass were analyzed along with data on host plant physiological condition and phenology. Spring population numbers of the South African psyllid *Acizzia russellae* were correlated with nitrogen levels in the leaves of its host, *Acacia karroo*. Also, populations were almost 10 times greater on the stump sprouts of cut trees than on leaves of uncut trees. In another study, aphid populations on 8 species of North American hardwoods showed similarly dramatic growth on stump sprouts following spring cutting. Homoptera which feed on cellular contents did not increase on cut plants, probably because leaf nitrogen concentrations were no higher than in uncut plants. Phloem feeding species, however, apparently responded mainly to the increased flow rate of nutrients in growing tissues of cut trees. Estimates of consumption using aphid densities from cut plants and literature values for ingestion were about 25%–50% of leaf standing crop. The uptake and cycling of such quantities, resulting from changes in plant condition, could have significant effects on plant function. These results clearly demonstrate that the condition of the host plant is a major factor influencing population densities in phloem feeding Homoptera, and suggest that feedback effects on plants may also be important.

Distribution of *Phyllonorycter* (= *Lithocolletis*) sp. in northeastern apple orchards. R. W. Weires and J. R. Leeper, Hudson Valley Lab., Highland, NY 12528

Surveys were conducted during 1976–1978 throughout Northeastern apple orchards to determine which leafminer species were responsible for recent outbreaks. Samples of leaves were collected from beneath the apple trees during the winter months. Apple branches and leaves were collected during the summer months from several New York, Connecticut, Vermont, and Massachusetts commercial orchards. All stages were either collected or reared from the leaf samples for specialists to examine. In addition, pheromone traps containing the *Phyllonorycter blancardella* sex attractant were deployed in several New York orchards and the adult males captured were saved for identification. *Phyllonorycter crataegella* was the predominant species found in Massachusetts, Connecticut, and the area East of the Hudson River in New York state. *Phyllonorycter blancardella* was the predominant species found in Western New York, the Champlain Valley, and Vermont. Both species were found in several orchards in Ulster, Greene, Saratoga and Washington counties of New York. The pheromone trap catches were predominately restricted to detecting the *Phyllonorycter blancardella* species with only very low numbers of *crataegella* found in the traps. Both species have strains which are not controlled by the present organophosphate insecticide programs.

Seasonal history of the leafhopper complex (Homoptera:Cicadellidae) on ornamental honeylocust. A. G. Wheeler, Jr. and K. Valley, Bureau of Plant Industry, PA Dept. Agric., Harrisburg, PA 17110

Leafhoppers have been included among the arthropods known to injure ornamental honeylocust. Since little biological data were available to implicate leafhoppers as pests, we studied the complex on 'Sunburst' honeylocust by sampling weekly the terminal 36 cm of 4 branches on 2 trees at Harrisburg, PA, during 1975–77. Four common species, exhibiting spatio-temporal differences were found: *Macropsis fumipennis*, *Stragania apicalis*, *Orientus ishidae*, and *Empoasca* sp. Eggs of *M. fumipennis* hatched shortly after leaf flush; nymphs fed on petiolules and rachises and were present from mid-April to late May. Adults matured in mid-May and persisted until late July. Large populations near the sample site, in the virtual absence of honeylocust plant bud (*Diaphnocoris chlorionis*), failed to produce the leaflet distortion characteristic of mirid injury. Nymphs of *S. apicalis*, present from late April to mid-May, fed mainly on leaflets. Although adults were found until September, we were unable to determine whether this species is bivoltine. Nymphs of *O. ishidae* were found from early June

to early July; adults, until late July. This introduced species fed on leaflets of water sprouts, yellowing the foliage. *Empoasca* adults, which appeared during June, may migrate each season into Pennsylvania. This leafhopper feeds mainly on the second flush of new growth and produces 2 or 3 generations by September. Our observations indicate that distortion of honeylocust foliage should be blamed on honeylocust plant bug, not on the petiolule-feeding *M. fumipennis* or other leafhoppers.

Physiological age study of five species of mosquitoes (Diptera: Culicidae) in southeastern New Hampshire. J. J. Winegar, Dept. of Entomol., Univ. of New Hampshire, Durham, NH 03824

Adult females of *Aedes excrucians*, *A. canadensis*, *A. cantator*, *A. vexans*, and *Coquilleltidia perturbans* were collected by human-bait capture, net sweeping, and CO₂-baited CDC light traps in Exeter, New Hampshire, from June to September, during 1978. Mosquito specimens were stored at -12°C for later dissection. Physiological age for 1,818 females was determined by the Polovodova method. The data revealed that females of each species could complete a minimum of two gonotrophic cycles. *A. excrucians* and *A. canadensis* had the greatest longevity, with 12.8% of *A. excrucians* and 10.9% of *A. canadensis* surviving to become 3-parous, one *A. canadensis* female was 4-parous. Females of *A. cantator*, *A. vexans*, and *C. perturbans* determined to be 2-parous were uncommon, comprising 0.6% to 3.0% of total number dissected. All species studied are anautogenous. Parity data showed that *A. excrucians* and *A. canadensis* were univoltine and emerged synchronously. *A. cantator* and *A. vexans* appear to have three distinct broods, while *C. perturbans* had a single brood, but emerged relatively asynchronously. *A. excrucians* and *A. canadensis* may be epidemiologically important in southern New Hampshire, particularly as potential vectors of dog heartworm, *Dirofilaria immitis*. Absence of multiple feeding in most *A. cantator*, *A. vexans*, and *C. perturbans* indicates these species probably played a very minor role as disease vectors in New Hampshire, in 1978, possibly due to extremely dry weather during the summer.

BOOK REVIEW

Comprehensive Virology 12. Newly characterized protist and invertebrate viruses. Heinz Fraenkel-Conrat and Robert R. Wagner, ed. Plenum Publishing Co., New York. 1978. 344 p. \$29.50.

This volume contains 5 chapters and entomologists will be particularly interested in the first and longest one, by T. W. Tinsley and K. A. Harrap, which provides a summary of viruses of invertebrates. The baculoviruses which comprise the nuclear polyhedrosis and granulosis viruses are already being used as "living insecticides" in the United States and in several other countries, because they differ from all viruses that infect higher animals and plants. They have normally a very narrow host range and their morphological characteristics are well illustrated by electron micrographs provided in this volume. Other groups of insect viruses, such as the entomopoxviruses, iridoviruses, the isometric RNA viruses to which the densovirus belongs and the rhabdoviruses are described in some detail. Main emphasis is on morphology because other characteristics have been studied to a lesser degree. An excellent review of the ecology and epizootiology is included in the first chapter and the literature citations comprise 20 pages. Unfortunately the chapter has been prepared several years ago and its publication delayed so that only a few references are as recent as 1975. This is especially regrettable since the authors, working at the Unit of Virology at Oxford, England, have made significant contributions in recent years and have characterized baculoviruses by modern techniques.

The remaining chapters describe viruses of fungi, cyanobacteria and pseudomonads, as well as the intriguing bacteriophages found in antibiotic-producing strains of *Penicillium*. The chapter on this subject is by T. I. Tikchonenko of the Ivanovsky Institute of Virology in Moscow, where most of this work has been done in recent years. A good subject index is provided.

Karl Maramorosch,
Waksman Institute of Microbiology,
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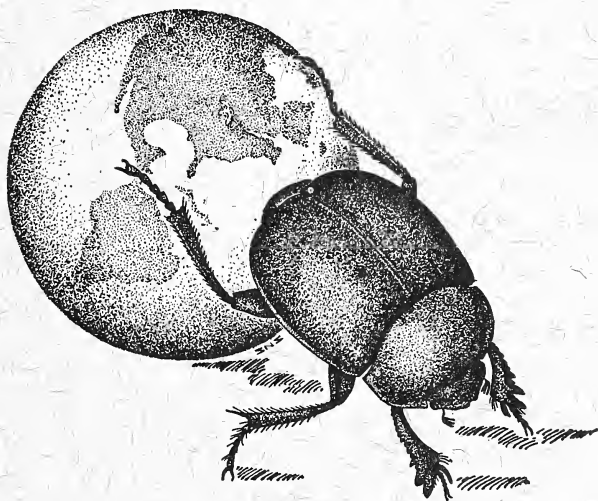
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ENVIRONMENTAL PARTITIONING IN LOWLAND TROPICAL
RAIN FOREST CICADAS

Allen M. Young

Abstract.—The peak emergence periods and habitats of cicadas were examined discontinuously over several years in lowland tropical rain forest of northeastern Costa Rica. Two distinctive ecological features of this region which might affect cicadas are (1) the existence of primary and secondary forest habitats, and (2) the occurrence of a short dry season. Although the data on adults concern six genera and eleven species, emphasis is placed on quantitative sampling of nymphal casts from ground plots for *Zammara smaragdina*, *Fidicina sericans*, *Fidicina mannifera*, *Fidicina pronoe*, *Fidicina spinocosta*, and *Quesada gigas*. If selection pressures favor emergence adaptations such as allochrony or habitat non-overlap among some species, it was expected that the census data would show these patterns. Generally the data support this hypothesis. For example, of the two most abundant cicadas, *Z. smaragdina* and *F. sericans*, the former emerges primarily during the long wet season while the latter emerges during the dry season. Both species occur in primary forest but *Z. smaragdina* also occurs in advanced secondary forest. Another, *F. mannifera*, is generally not very abundant, has low emergence almost continuously throughout the year, and sings at times of the day when others are less active. Others such as *F. spinocosta* and *F. pronoe* and *Q. gigas* emerge in young secondary forests but in different seasons. Owing to the high selective value placed upon the cicada song in breeding, temporal and spatial partitioning of the environment may be an adaptive measure that reduces interspecific competitive conflicts that could arise by adults of abundant species being active at the same times of the year or in the same habitats.

Introduction

This paper reports the peak emergence periods and habitats for several genera and species of cicadas (Homoptera: Cicadidae) in the lowland tropical rain forest of northeastern Costa Rica. While six genera and eleven species of cicadas occur in this region (Young 1972; pers. obs.), quantitative data on emergences were obtained for three genera and six species: *Zammara smaragdina* Walker, *Fidicina mannifera* (Fabricius), *Fidicina sericans* Stal, *Fidicina spinocosta* (Walker), *Fidicina pronoe* (Walker), and *Quesada gigas* (Olivier) (Figs. 1-4). These are large-bodied cicadas that were previously determined (pers. obs.) to occupy different habitats (Table



Fig. 1. *Zammara smaragdina*; female, male, male (lateral view). This is a loud and large-bodied green-and-brown cicada of the Caribbean lowland tropical rain forest.

1). Owing to the availability of several distinct habitats and a pronounced dry season (e.g., Slud 1974), it was predicted that different species may exhibit different habitat preferences and annual periods of peak emergences if they were in competition for some resources. While this study did not determine these resources, the data indicate considerable allochrony and non-overlap in habitat for these cicadas.

Region and Habitats

The cicadas were studied at "Finca La Tirimbina," near La Virgen de Sarapiquí (220 m elev.), Heredia Province. The site is a 1,000-acre farm complex with primary forest (mostly fragmented into remnants) and a variety of secondary forest habitats. The dominant tree in the primary forest remnants is *Pentaclethra macroloba* (Willd.) Ktze. (Leguminosae) whose life history has been described by Hartshorn (1975). Advanced secondary forest (over 25 years old) is dominated by trees of *Goethalsia meiantha*



Fig. 2. *Majeorona bovilla* and *Fidicina mannifera* (left to right) are large, black-and-brown-bodied cicadas of primary forest; their songs are loud and *F. mannifera* sings primarily at dawn and dusk.

(Donn. Sm.) Burret (Tiliaceae) forming a canopy of about 25 m (DBH = 9 cm) and with a dense understory of *Pentaclethra* seedlings and saplings. Young (2–10 years old) secondary forest contain a large number of woody shrubs and treelets (canopy less than 4 m) such as *Vernonia patens* H.B.K. (Compositae) and *Vismia guianensis* (Aubl.) Pers. (Guttiferae). A short dry season falls between January and April (Frankie et al. 1974). Generally the rainfall is less than 225 mm per month during the dry season, especially in March and April (Fig. 5). The pattern shown in Figure 5 is typical for several years (e.g., 1971–78) (pers. obs.).

Census Methods

Population size, density, and sex ratio were obtained for each cicada species by collecting nymphal casts from plots of known size. The majority of cicada censuses were taken between June 1972 and July 1974, although a few additional ones were made in 1976 and 1978. These censuses were



Fig. 3. Left to right: *Fidicina sericans*, *F. pronoe*, *F. amoena*, and *F. spinocosta*. With the exception of *F. sericans*, these cicadas occupy young secondary forest. *Fidicina sericans* and *F. pronoe* are black-bodied and they are active primarily in the dry season; *F. amoena* and *F. spinocosta* are green-bodied wet season species and the latter sings primarily at dusk.

discontinuous and were timed to sample habitats at different times of the year. *Zammara smaragdina* was censused in 23 nested quadrats (see "quadrat area" in Fig. 6), each 6 by 5 meters, located on a hill covered with *Goethalsia* (advanced secondary forest—Fig. 7) for a total of 30 days over the three years. Eleven additional scattered quadrats of the same size, each one around a large *Pentaclethra* in forest remnants (Fig. 8), were used to census *Z. smaragdina*, *F. mannifera*, and *F. sericans* for a total of 28 days in the same period. Several other isolated plots of varying size ("road-edge plot"—6 by 5 m; "hill-top plot"—9 by 6 m; "river-edge plot"—12 by 8 m) were established in different types of secondary forest (Fig. 6) to census *F. spinocosta* and others. A total of 34 days were spent censusing nymphal casts from these three plots. *Fidicina pronoe* was censused (March 1976) in a pasture covered with *Vernonia* shrubs and following a brief dry season census of *Z. smaragdina* in the "quadrat area"; *Quesada gigas* and *F.*

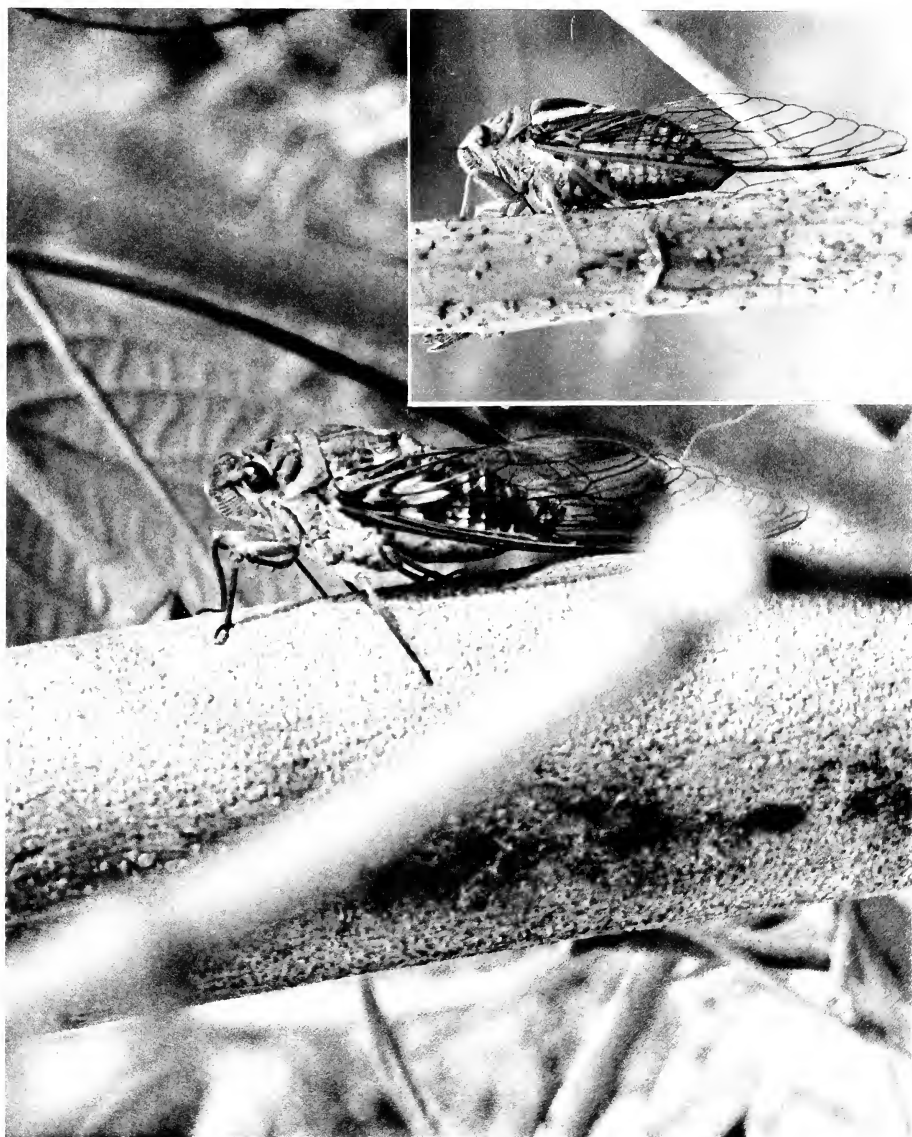


Fig. 4. *Quesada gigas* and *Fidicina pronoe* (inset) feeding at branches of *Vernonia patens* (Compositae) in young secondary forest during the dry season, a time of peak emergence of these species.

pronoe were censused in February 1978 in a plot (20 by 10 m) in a grove of nutmeg trees, *Myristica fragans* Houttuyn (Myristicaceae). During most censuses, two or three trained workers collected nymphal casts together from each quadrat or plot. The nymphal casts of different cicadas were

Table 1. Habitat associations of adult cicadas in northeastern Costa Rica, below 250 m elevation.

Primary forest	Body length (mm)	Advanced secondary forest	Body length (mm)	Young secondary forest	Body length (mm)
<i>Zammara smaragdina</i> Walker	35-37	<i>Zammara smaragdina</i> Walker	35-37	<i>Fidicina pronoe</i> (Walker)	30-32
<i>Fidicina sericans</i> Stal	33-36			<i>F. spinocosta</i> (Walker)	30-31
<i>F. mannifera</i> (Fabricius)	38-39			<i>Quesada gigas</i> (Olivier)	39
<i>F. amoena</i> Distant	30-33				
<i>Carineta indecora</i> (Walker)	12-13				
<i>Majeorona bovilla</i> Distant	38-39				
<i>Proarna sallei</i> Stal	21-22				

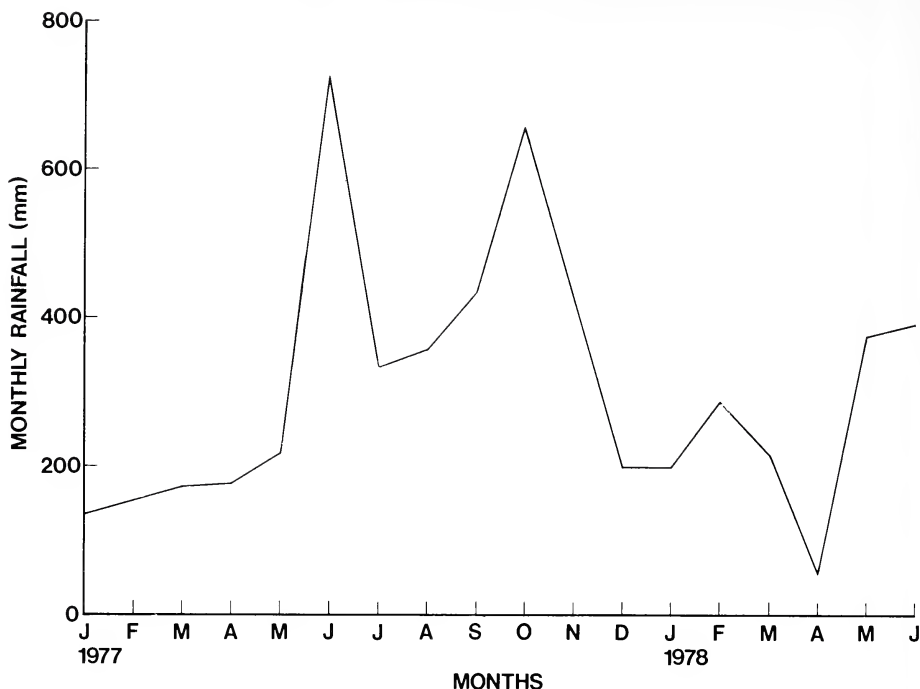


Fig. 5. The rainfall pattern at "Finca La Tirimbina" during a one and one-half year period (data courtesy of Dr. J. Robert Hunter). A dry season occurs between January and April, with monthly rainfall during these months usually falling below 225 mm. The patterns shown are typical for several years in this region.

readily distinguishable from one another (see also Young 1972), facilitating field censuses.

Results

Habitat Separation by Adult Cicadas

Of eleven species that occur in this region, adults of seven were seen and heard in primary forest remnants, and these species comprise the greatest range in body length (Table 1). Only one cicada, *Z. smaragdina*, overlaps with other habitats, namely advanced secondary forest and the highest number of congeneric species occurs in primary forest (Table 1). In primary forest, adult *Z. smaragdina* feeds on, and choruses from *Pentaclethra* trees, as does *F. sericans*. In advanced secondary forest, the former species is similarly associated with *Goethalsia* trees. Where this habitat is contiguous with primary forest, sometimes dense aggregations of *F. sericans* adults are

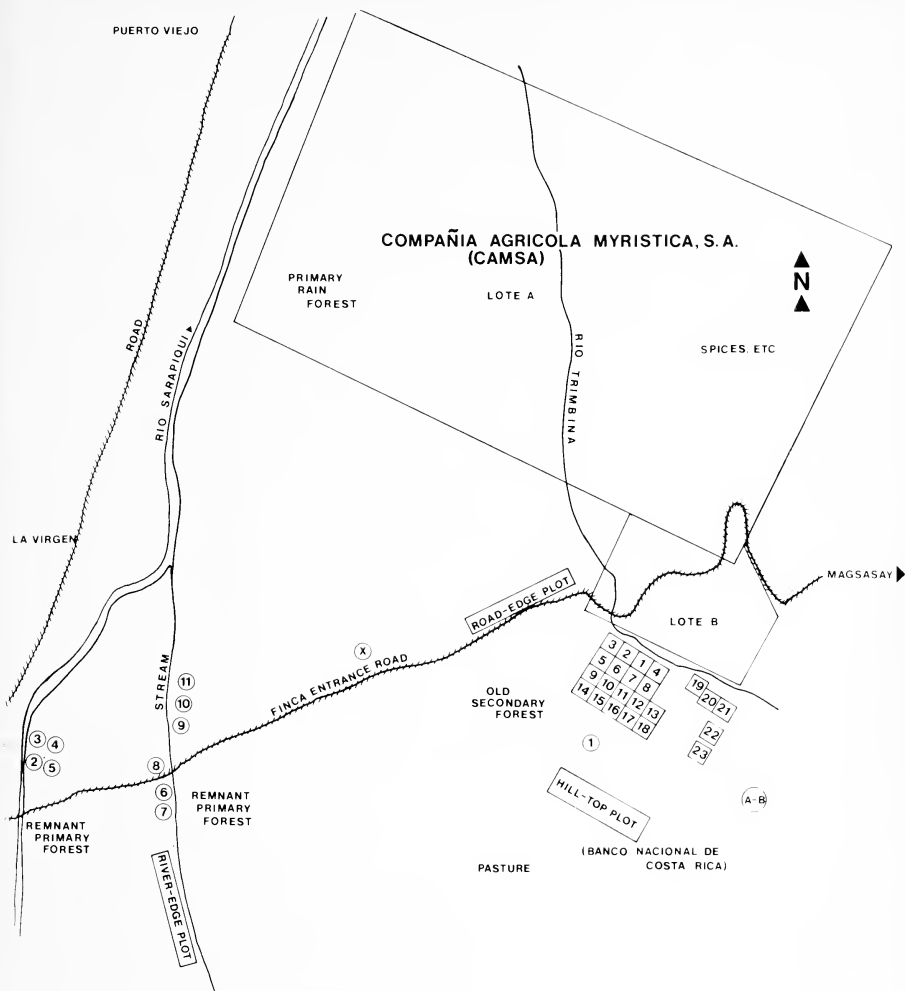


Fig. 6. The areas used to examine cicada emergences: (a) "quadrat area" on a *Goethalsia*-covered slope along the Rio Tirimbina (positions of quadrats shown by the numbered squares); (b) a series of large *Pentaclethra* trees in primary forest, shown here by numbered or lettered circles; (c) three large "plots" as indicated here. The areas designated as "lote A" and "lote B" indicate sites of cultivation for crops such as cocoa, black pepper, nutmeg, etc. Modified version of a map provided by Dr. J. Robert Hunter.

seen in *Goethalsia* trees. In some patches of advanced secondary forest there are feeding aggregations of *F. mannifera*, *F. sericans*, and *Z. smaragdina* on *Zanthoxylum procerum* Donn. Sm. (Rutaceae). Both *F. sericans* and *Z. smaragdina* oviposit in seedlings of *Pentaclethra* in primary forest,



Fig. 7. The *Goethalsia*-covered "quadrat area" where *Zammara smaragdina* was censused.

while the former also oviposits in a variety of understory woody shrubs in advanced secondary forests. In young secondary forests, *Q. gigas* and *F. pronoe* feed and oviposit in shrubs of *Vernonia* and occasionally in *Inga* sp. (Leguminosae). *Fidicina spinocosta* adults are associated with a wide range of woody shrubs including *Vismia*. *Carineta indecora* is a small cicada associated with the primary forest understory (Young 1972), especially near light gaps, while *F. amoena* is most frequently heard in large trees along streams in primary forest. *Majeorona bovilla* adults occur in patches along borders of primary forest and *Proarna sallei* choruses in tall *Cordia alliodora* (R. & P.) Oken. (Boraginaceae) along the borders of primary forest (see also Young 1972).

Some cicadas exhibit pronounced seasonality in adult activity as indicated primarily by chorusing activity. The greatest number of chorusing *Z. smaragdina* are heard during the mid-wet season, especially in July–August while intense chorusing in *F. sericans* takes place in the late dry season, especially March–April. Others, such as *F. pronoe* and *Q. gigas* are most

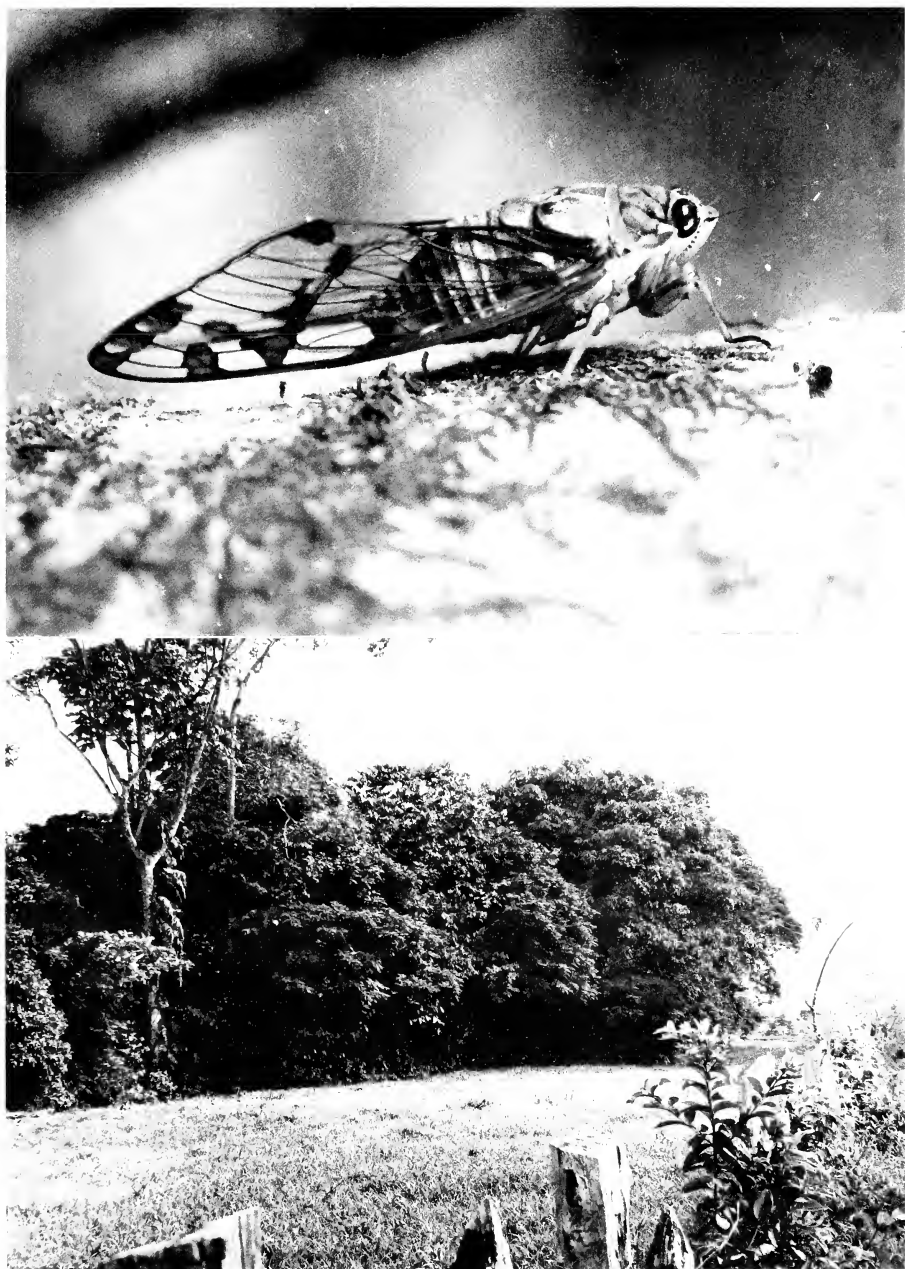


Fig. 8. *Zammara smaragdina* (female). Below: primary forest remnants dominated by *Pentaclethra* are habitats for *Zammara smaragdina*, *Fidicina sericans*, *Fidicina mannifera*, and *Majeorona bovilla*.

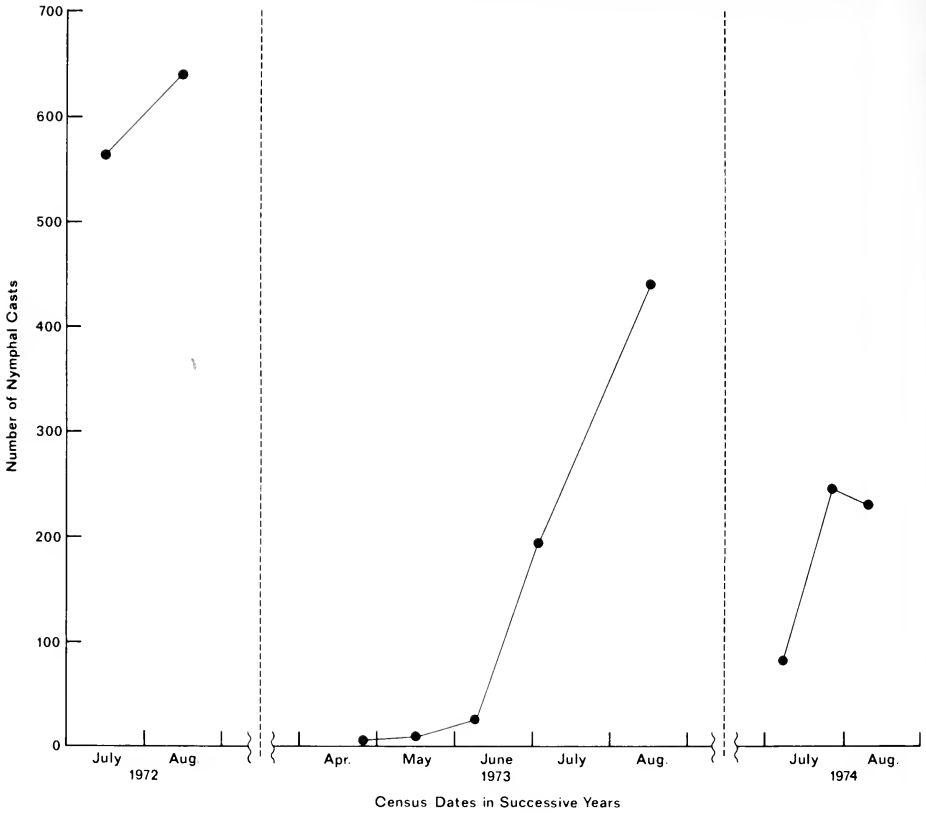


Fig. 9. Peak emergence periods for *Zammara smaragdina* in the "quadrat area" for three successive years. Peak numbers of nymphal casts appear in mid-wet season, July and August, each year.

active near the end of the dry season (April); *F. spinocosta*, *F. amoena*, *C. indecora* and *M. bovilla* are active during the wet season. Two cicadas, *F. mannifera* and *P. sallei*, are generally heard throughout the year but with some diminishing activity in November–December. In summary, of the eleven species seven are active during the wet season (including two which are active throughout the year); the wet season generally lasts eight months. Although *F. mannifera* adults are active in the same habitat with *F. sericans* and *Z. smaragdina* and at the same times of the year, chorusing intensity is greatest in the early evening (5:00–6:00 P.M.) in the former cicada. Most of the other cicadas chorus throughout the day, although *F. spinocosta* and *Q. gigas* often exhibit pronounced bursts of activity near dawn and dusk. In fact, while *F. pronoe* generally sings throughout most of the day and occasionally near dusk, *Q. gigas* in the same habitat exhibits a large burst of singing at dusk and sings only sporadically during the day.

Table 2. Some emergence parameters for the cicada *Zammara smaragdina* in 23 quadrats (each 5×6 m) in advanced secondary forest in northeastern Costa Rica.

Census date	Season	No. casts in quadrats				Mean no. casts in quadrats				Range in no. casts in quadrats			
		♀♀	♂♂	?	T	$\bar{x} \pm SE$ ♀♀	$\bar{x} \pm SE$ ♂♂	$\bar{x} \pm SE$ T		♀♀	♂♂	T	
July 14-17, 1972	Wet (Late)	259	262	43	564	11.26 \pm 8.28	11.39 \pm 8.47	24.52 \pm 16.81		0-38	1-29	1-71	
Aug. 12-13, 1972	Wet (Late)	343	250	51	644	14.91 \pm 18.54	10.82 \pm 10.75	28.00 \pm 30.61		0-73	0-42	1-114	
Apr. 21-22, 1973	Dry (Late)	1	1	0	2	0.04 \pm 0.20	0.04 \pm 0.20	0.08 \pm 0.28		0-1	0-1	0-1	
May 11-16, 1973	Wet (Early)	2	5	0	7	0.08 \pm 0.28	0.21 \pm 0.42	0.30 \pm 0.55		0-1	0-1	0-2	
June 1-5, 1973	Wet	3	19	0	22	0.13 \pm 0.34	0.82 \pm 1.15	0.95 \pm 1.22		0-1	1-4	1-4	
July 1, 1973	Wet	91	104	1	196	3.95 \pm 4.81	4.47 \pm 4.95	8.47 \pm 9.35		0-21	0-18	1-39	
Aug. 12-13, 1973	Wet (Late)	257	173	0	430	11.17 \pm 8.64	7.52 \pm 5.95	18.69 \pm 14.29		0-35	1-23	1-58	
July 3-4, 1974	Wet	35	43	0	78	1.52 \pm 2.10	1.86 \pm 2.24	3.39 \pm 3.93		0-7	0-8	0-12	
July 27-28, 1974	Wet	135	113	0	248	5.86 \pm 5.64	4.91 \pm 6.97	10.78 \pm 11.89		0-22	0-33	0-55	
Aug. 8-9, 1974	Wet (Late)	123	108	0	231	5.34 \pm 5.31	4.69 \pm 4.66	10.04 \pm 9.76		0-17	0-17	0-34	

* Damaged or crushed casts in which sex could not be determined.

Patterns of Cicada Emergences

The highest number of nymphal casts of *Z. smaragdina* were found during mid-wet season (July–August) and very few during the late dry season (March–April) and the emergences declined over the three years (Fig. 9). Although these data are discontinuous (Fig. 9), visits to the area following periods when no censuses were taken revealed the same abundance. The number of cicadas emerging from each quadrat varied considerably on each census date (as much as 100-fold) and the sexes occurred equally (Table 2). A few quadrats consistently yielded the greatest numbers of cicadas; of the 2,418 cicadas emerging from the area over three years, about 15% came from quadrat no. 23. Other quadrats produced less than ten cicadas each year, and overall the area produced about 3.5 cicadas per square meter for the study period or about one cicada per square meter each year. All nymphal casts censused in the area were *Z. smaragdina*.

The mean number of nymphal casts of this cicada obtained from the *Pentaclethra* trees was 19.37 ± 31.18 (SE; $N = 11$) for the same period, and this figure is within the range of mean values for the "quadrat area" during periods of peak emergence (Table 2). However, *Fidicina sericans* was the most abundant cicada emerging at *Pentaclethra*, producing 28.46 ± 48.99 nymphal casts per tree during the late dry season, while *F. mannifera* was far less abundant producing 4.1 ± 6.5 nymphal casts for the same trees and period. Although the sample size of *Pentaclethra* is small, *F. sericans* emerged at all eleven trees, while *Z. smaragdina* at eight, and *F. mannifera* at four. Subsequent anecdotal observations (e.g., January–February 1976) indicated that although *Z. smaragdina* peaks in emergence in the wet season and *F. sericans* during the late dry season, a few fresh nymphal casts of the latter have been collected during brief dry periods amid an otherwise wet season. Likewise, a few *Z. smaragdina* emerge during brief rainy periods during the dry season.

In some areas of primary forest, dense emergences of *F. sericans* were observed during the dry season. For example, during a five-week period in the 1975 dry season, 903 nymphal casts of this cicada (9.3 cicadas per square meter) were collected from the "river-edge plot" (Fig. 6) while only 1,800 nymphal casts were collected from the *Pentaclethra* over three years (5.4 cicadas per square meter). The river-edge emergence of this cicada represented a ten-fold increase when compared to the emergence of *Z. smaragdina* in the "quadrat area."

Fidicina spinocosta emerges during the wet season in young secondary forest areas such as the "road-edge plot" (Fig. 7) where 120 nymphal casts (1.5 cicadas per square meter) were collected in 1973 and 1974 (seven collections); most of these were clumped around two *Vismia* trees. Another 148 nymphal casts (two collections) were collected in the 1974 wet season

from the "hill-top plot" (Fig. 7) (2.7 cicadas per square meter). Seventy-five nymphal casts of *Z. smaragdina* and one each of *F. sericans* and *F. mannifera* were also collected from this plot during the same period. Two other cicadas, *F. pronoe* and *Q. gigas*, emerge in young secondary forest habitats, but in ones that are abandoned pastures overgrown with the shrub *Vernonia*. *Fidicina spinocosta* and the other cicadas mentioned above emerge in areas containing a great variety of woody shrubs and treelets. The census of 15 *Vernonia* in a field produced 53 nymphal casts of *F. pronoe* (4.5 ± 3.7 per tree), while eleven nymphal casts of *Q. gigas* were also found. The census in the nutmeg grove produced 24 *F. pronoe* and 14 *Q. gigas*.

Discussion

The data indicate that different species of cicadas occurring in a lowland tropical rain forest region occupy different habitats and have different peak emergence periods each year. The primary forest contained the largest number of cicada species. Furthermore, the body size range of these species is greater than for species in secondary habitats. The range in body sizes in insect species might be an indicator of a larger number of ecological niches available (Schoener and Janzen 1968). Secondary habitats tend to support fewer cicada species and this was also the case for advanced secondary forest regions in the mountains of central Costa Rica (Young 1975).

Other studies have shown that insects and plants exhibit seasonal responses to changes in rainfall, timing various activities with a particular season (e.g., Janzen 1967; Schoener and Janzen 1968; Frankie et al. 1974). This study and a previous one (Young 1972) show that different species of cicadas may have allochronic emergences that result in breeding activities (courtship, mating, oviposition) also being allochronic among the species. The emergence of a greater number of cicada species in the wet season may be a result of this period being longer than the dry season in this region. The factors responsible for triggering cicada emergences in the tropics have not been determined. Perhaps a drying out of the soil acts as a proximal cue for the emergence of *F. sericans*, *F. pronoe*, and *Q. gigas* late in the dry season. Increased rainfall and soil moisture content in the wet season may be a cue for the emergence of *Z. smaragdina*, *F. spinocosta*, and others. The two most abundant cicadas, *Z. smaragdina* and *F. sericans* emerged from the same patches of primary forest and the former also emerged in advanced secondary forest. The discovery that peak emergences in these species are allochronic suggests a temporal partitioning of the environment that results in breeding activities taking place at different times each year. A similar pattern exists for cicadas such as *F. spinocosta* and *F. pronoe* in young secondary forest habitats.

The emergence data also suggest that when two cicadas have similar abundance levels in the same habitat, they tend to have highly allochronic or seasonal emergences. But a species such as *F. mannifera*, with relatively low emergence in a given month, although emerging in the same forest patches as *F. sericans* and *Z. smaragdina*, is essentially active throughout most of the year. Even though *F. mannifera* is active with two or more congeneric species at the same time, it sings primarily at times of the day when the others do not. The data also show that a similar daily partitioning of daylight hours for singing takes place between two late dry season cicadas in the same habitat, *F. pronoe* and *Q. gigas*.

Certain types of microhabitats within the primary and secondary forest habitats may provide very suitable conditions for cicada development and survival. *Pentaclethra* is one of the most abundant trees in lowland tropical rain forests of Costa Rica (Hartshorn 1975) and the present study and a previous one (Young 1972) have shown that cicadas often emerge near them. Other suitable microhabitats for cicadas in this region are patches of *Goe-thalsia* in advanced secondary forests and patches of *Vernonia* and *Vismia* in young secondary forests. North American periodical cicadas have been shown to have definite habitat and microhabitat associations (e.g., Dybas and Lloyd 1962, 1974) as do some non-periodical species in the same region (Moore 1966). The types of trees and shrubs present in an area may determine the availability of suitable oviposition sites and nymph development sites for cicadas in tropical habitats. The observed large differences in number of nymphal casts collected in different quadrats in the same area also suggest environmental heterogeneity affecting cicada oviposition and/or development within the habitat.

Although the proximal factors determining the observed patterns of environmental partitioning by cicadas were not investigated, such patterns could be explained by selection pressures resulting from a limited availability of resources. Such selection pressures would involve the determination of physiological and behavioral responses of mature cicada nymphs to changes in environmental factors indicating season and act to time the peak emergence with either the wet or dry season. Allee et al. (1949), among others, emphasize the role of limited resources in resulting in selection pressures expressed through interspecies competition. If, for example, in the present study, suitable singing, feeding, and/or oviposition sites are limited resources for cicadas in tropical habitats, selection may result in allochronic emergence patterns among some species occupying the same habitats, or cause divergence in habitat occupancy among species active during the same time of the year. An additional factor might be the continued cutting down of primary forest, favoring those cicadas that occupy secondary forests.

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Invertebrate Division, Milwaukee Public Museum, Milwaukee, Wisconsin 53233.

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SIMULTANEOUS USE OF A FORAGING TRAIL BY TWO
LEAFCUTTER ANT SPECIES IN THE
SONORAN DESERT

Alex Mintzer

Abstract.—An episode of simultaneous utilization of a foraging trail by two attine ants, *Acromyrmex versicolor* (Pergande) and *Atta mexicana* (F. Smith), is described. No aggressive behavior between the two species was noted, except near an *Acromyrmex* nest entrance. This observation of simultaneous trail use is of particular interest because both species have similar habits and they overlap in selection of food plant species in the Sonoran Desert.

Acromyrmex versicolor (Pergande) is a common leafcutting ant in the desert regions of Arizona and Sonora. The natural history and foraging behavior of this ant has been described by Wheeler (1907) and Gamboa (1975, 1976). The leafcutting ant *Atta mexicana* (F. Smith) ranges from extreme southern Arizona through most of Mexico (Smith 1963). Both species culture fungi and they occur at a study site 46 km south of Sonoita, Sonora, Mexico. The foraging behavior of *Atta mexicana* at this site has been described (Mintzer 1979).

Both ant species cut material from annual and perennial plants and collect dry vegetation. *Atta mexicana* and *Acromyrmex versicolor* exhibit a broad overlap in their selection of target plant species. They cut pieces from the winter annual *Plantago insularis* Eastwood when it is available, and utilize fresh and dry material from the common large desert perennials *Larrea tridentata* Coville, *Olneya tesota* Gray, and *Prosopis velutina* Woot. Their temporal periods of foraging activity are very similar. Both species forage during the day in winter and spring (1974-77; 24 days total observation period).

These mycophagous ants use trails as a regular component of foraging activity. On March 25, 1977, simultaneous use of a 6-8 m trail segment by these two species was noted by the author and field assistant Barry Pullen. Both ant species were collecting leaf pieces from creosote bush, *Larrea tridentata*, and *Plantago insularis*. The trail extended along the side of an arroyo channel. The slope was rough but generally free of debris, and the ants made no effort to clear or level the trail surface. The trail was 6-10 cm wide; trails of *Atta mexicana* are usually 3-5 cm across (unpub. observation), while those of *Acromyrmex versicolor* are up to 14 cm in width (Gamboa 1975). One end of the trail terminated at a nest opening of the *Acro-*



Figs. 1, 2. 1. Section of trail used by *Atta mexicana* and *Acromyrmex versicolor*. Lower left: *Acromyrmex versicolor* forager with cut item from *Plantago insularis*. Upper right: *Atta mexicana* forager with cut leaf from *Larrea tridentata*. 2. Another section of the trail. From lower left to upper right: *Acromyrmex versicolor*; *Atta mexicana*; *A. mexicana* (submajor with forage item); *Acromyrmex versicolor*; *A. versicolor* (with forage item). *Atta mexicana* foragers have longer legs than the *Acromyrmex versicolor* foragers of comparable size.

myrmex colony, which was surrounded by a pile of cut pieces from *L. tridentata*. *Acromyrmex* workers were returning to this nest entrance with forage items during the period of observation, while *Atta* workers with forage items traveled in the opposite direction, towards their own tunnel opening (see figures). *Acromyrmex* workers attacked and chased *Atta* foragers they encountered on this pile or near the nest entrance. B. Pullen observed six dead or injured *Acromyrmex* and one dead *Atta* worker near this entrance. Most *Atta* workers left the trail about 60 cm from the *Acromyrmex* nest entrance and foraged individually, returning to the trail after securing leaf pieces. Foragers of both species were well represented when the trail was first noted around 1300 hr local time. Seventy *Acromyrmex* and 66 *Atta* workers passed a fixed point on the trail during a five minute period. No aggressive interactions were noted on the trail, except within 25 cm of the *Acromyrmex* nest opening. However, *Atta* became less abundant on the trail later in the afternoon.

The *Atta* colony involved in this episode produced up to 30 trails simultaneously, and at least two *Acromyrmex versicolor* colonies were located near the margins of its foraging area. The one episode of simultaneous use of a trail occurred shortly after a period of rain, when *Acromyrmex* was very active on the surface. The *Atta* foragers may have initially been attracted to the accumulation of *L. tridentata* leaf pieces around the *Acromyrmex* nest entrance. From my observations, it was impossible to determine whether both species are capable of following each other's trails, or which ant produced the initial trail.

In the laboratory, some attine species follow trails produced using abdominal gland extracts from other attine species and genera. In *Atta texana* (Buckley), the poison gland in the abdomen is the source of the primary trail pheromone (Blum et al. 1964; Moser 1967). Moser notes: "In the field, however, although the trails of various species cross, the workers generally find their own trails easily." For a more typical account of relations between foragers of two *Atta* species, check Weber (1969). At the study site in Mexico, *Acromyrmex* was active on only a few observation days, and trails of the two species were not observed near each other on other occasions when simultaneous foraging activity occurred.

Wilson (1965) describes a case of simultaneous trail use by two ants on Trinidad, and reviews two cases discovered by W. M. Wheeler in neotropical forest. In two of these cases involving *Crematogaster limata parabiotica* Forel [with *Camponotus femoratus* (Fabricius) and *Monacis debilis* (Emery)], some of the shared trails led to food resources such as membracids used by both ants involved, and no aggressive interactions were noted. In the third case, *Camponotus beebei* Wheeler utilized trails of *Azteca chartifex* Forel, and some aggressive interactions were noted on the trails.

In all of these reports, the two ant species involved belong to different subfamilies (Myrmicinae, Dolichoderinae, or Formicinae). In contrast, *Atta* and *Acromyrmex* are closely related myrmicine genera (Weber 1972). Simultaneous use of a foraging trail is particularly interesting in this case because the species involved are members of a smaller and more recently evolved phyletic group with similar and unique dietary habits, and they may be expected to compete for resources where they occur together.

Acknowledgments

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Museum of Zoology and Division of Biological Sciences, The University of Michigan, Ann Arbor, Michigan 48109.

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CAUSES OF LIFE HISTORY DIFFERENCES BETWEEN THE
MORPHS OF *PEMPHIGUS POPULITRANSVERSUS*¹

Lorenz Rhomberg

Abstract.—The aphid *Pemphigus populitransversus* produces galls of two distinct morphs on cottonwood petioles. There are pronounced between-morph differences in both the number and maturity distribution of aphids within the galls. The progress of gall maturation was followed over the summer to determine whether these life history differences are explainable solely by the fact that galls of the “globular” morph are initiated some seven weeks later than those of the “elongate” morph or whether qualitative differences exist in the pattern of gall maturation. It was found that the *pattern* of maturation for the two morphs was similar, with globulars being always seven weeks behind. However, the *number* of nymphs and mature alates was about three times greater in globular galls.

Introduction

Pemphigus populitransversus Riley is a gall-forming aphid attacking leaves of cottonwoods, principally *Populus deltoides* Marshall and *P. sargentii* Dode. A nymphal stem mother hatches from a sexually produced egg in the spring and initiates a gall on a cottonwood petiole. The growing petiole tissue quickly encloses her in a capsule within which she parthenogenetically and viviparously produces nymphal fundatrigeniae which, as winged adults, leave the gall and fly to secondary hosts of the family Cruciferae.

In the study of a dimorphism of galls in this aphid Senner and Sokal (1974) found large differences in the numerical distribution of developmental stages in the two morphs. In fact, they noted that “the two samples can be differentiated on life history characteristics more clearly than on gall shape, the initial criterion for separation [into two morphs]” (p. 368). Galls of the “globular” morph contained fewer nymphs, most (98.1%) of which were in the smallest of three size classes. Galls of the “elongate” morph had about half their nymphs in the two largest size classes and had more alates (adult fundatrigeniae). Senner and Sokal hypothesized that “nymphs in the ‘globular’ galls . . . , although necessarily born sequentially, develop synchronously and . . . the bulk of alate production must be in the late fall. In the

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'elongate' sample . . . the nymphs seem to develop sequentially throughout the summer with alates presumably being produced continuously'' (p. 368).

Subsequently, Faith (1979a) discovered that the globular-elongate dimorphism was based on different times of gall initiation. Elongate galls are initiated in early May by stem mothers hatching from overwintering eggs. They are formed on the early flush of leaves (which are pre-formed in the bud) soon after bud-break. Globular galls are founded by stem mothers hatching some six weeks later from eggs that are laid in the spring. These galls are on the second, morphologically distinct, flush of leaves (Faith 1979a). The ranges of the two morphs seem to overlap essentially completely (Bird et al. 1979).

Faith (1979b) proposed that this difference in time of gall initiation provides a simple alternative to Senner and Sokal's explanation of the life history differences between the morphs. He showed that globular galls produced their first alates during the first days of August—again six weeks later than elongate galls attain this milestone. Perhaps globular galls are simply less mature, and at the time of collection of Senner and Sokal's original dimorphic sample (August 5, 1966 in West Point, Ga.) even the oldest nymphs were still small. The differences in the mean and variance of the distribution of life history stages should then disappear later on in the season.

It is the purpose of this paper to show that differences in gall age between the morphs can indeed account for the life history dimorphism discovered by Senner and Sokal. There is some evidence, however, that some developmental synchrony may exist in globular galls, but on a scale much smaller than Senner and Sokal originally envisaged.

Materials and Methods

Galls of *Pemphigus populitransversus* were collected at roughly weekly intervals from a mid-sized (approximately 15 cm dbh) eastern cottonwood tree (*Populus deltoides*) in Port Jefferson, L.I., N.Y. Five elongate galls were collected each time beginning on 13 June 1975 and ending on 7 September 1975. Five (occasionally six) globular galls were collected each time beginning on 31 July 1975, and ending on 4 October 1975. Galls could be assigned to one or the other morph unambiguously by noting whether they were on early or late leaves. Galls were immediately preserved in 70% ethanol. Later, each gall was opened and censused for the number of small, medium, and large sized nymphs, as well as the number of alates. Procedures were those of Senner and Sokal (1974).

Abbreviations and definitions of variables are listed in Table 1. Several empty or parasitized galls were eliminated from further study. Since Senner and Sokal coded the numbers of nymphs in each size category into 10 abun-

Table 1. Variables used in this study.

Abbreviation	Definition
# SM NYM	The number of "small" nymphs in the gall, roughly those in the first or second instar.
# MD NYM	The number of "medium" nymphs in the gall, roughly those in the third, or penultimate, instar.
# LG NYM	The number of "large" nymphs in the gall, roughly those in the fourth, or ultimate, instar.
# ALATES	The number of adult fundatrigeniae in the gall.
G LH MN	By coding small, medium and large nymphs as 1, 2 and 3 respectively, the mean nymphal stage attained by all nymphs in the gall. Coded abundances of each stage were used. ¹
G LH VAR	By coding small, medium and large nymphs as 1, 2 and 3 respectively, the variance in nymphal stage attained by all nymphs in the gall. Coded abundances of each stage were used. ¹

¹ Abundances were coded into 10 classes following Senner and Sokal (1974): 0: 0 nymphs, 1: 1–10 nymphs, 2: 11–20, 3: 21–30, 4: 31–40, 5: 41–50, 6: 51–60, 7: 61–70, 8: 71–80, 9: 81 and greater.

dance classes, the mean developmental stage and its variance (G LH MN and G LH VAR respectively) were calculated for each gall using their coding scheme. I have reported the nymph abundances themselves as uncoded counts, however.

Results

The changes in variance in developmental stage attained (G LH VAR) over the season are plotted in Figure 1. During June the variance for elongate galls shows a sharp rise as the first nymphs mature. By July 1 a maximum variance (and mean) of the distribution is attained, and remains at that level until September (at which time the supply of elongate galls was exhausted). Alates are continually leaving the gall during this time, so the stable mean and variance represent a steady state distribution of developmental stages.

Globular galls progress along an essentially identical curve, save that it is *displaced* some 50 days later in the season. The initial rise is about as rapid as for elongates, and the same steady state is maintained from then on, at just the same level, until leaves drop in the autumn.

Figure 2 shows the progress of gall population size over the season, with each bar divided according to the numbers present for each developmental stage. The maximum population size of globulars is much greater than that of elongates. This maximum is attained more quickly (and lost more quickly)

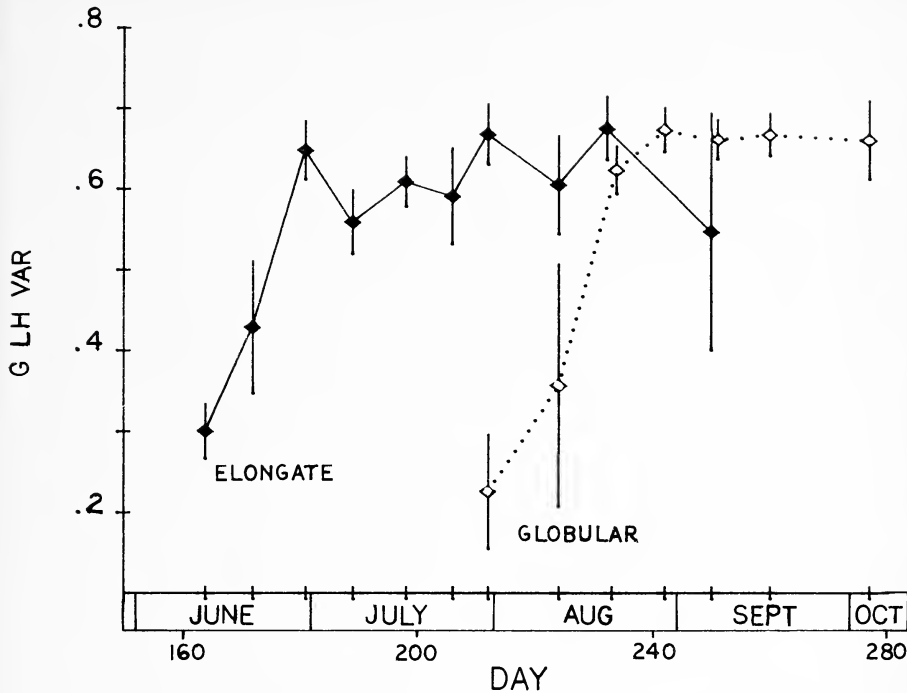


Fig. 1. Changes in life history variance (the variance of the distribution of maturities) in elongate galls (solid points) and globular galls (open points). Vertical bars indicate \pm one standard error of the mean. Sample sizes may be obtained from Figure 2. Abscissa is number of days since January 1, 1975.

than in elongates. It should be noted that at the end of the initial, essentially “all small nymph” stage, globular galls have already attained about one third of their eventual peak population, whereas elongates have only reached about one seventh of their maximum at the analogous time. Furthermore, the initial phase of increase in life history variance is accompanied by rapid population size increase in elongates, but not so in globulars. Instead, the rapid increase in population just follows the attainment of the stable distribution of life history stages.

Discussion

At any given time until mid-August galls belonging to the globular morph will indeed have a very different distribution of developmental stages than those of the elongate morph, as noted by Senner and Sokal. These differences seem to be a consequence of the different ages of galls of the two morphs at any one time. They vanish in mid-August as globular galls “catch

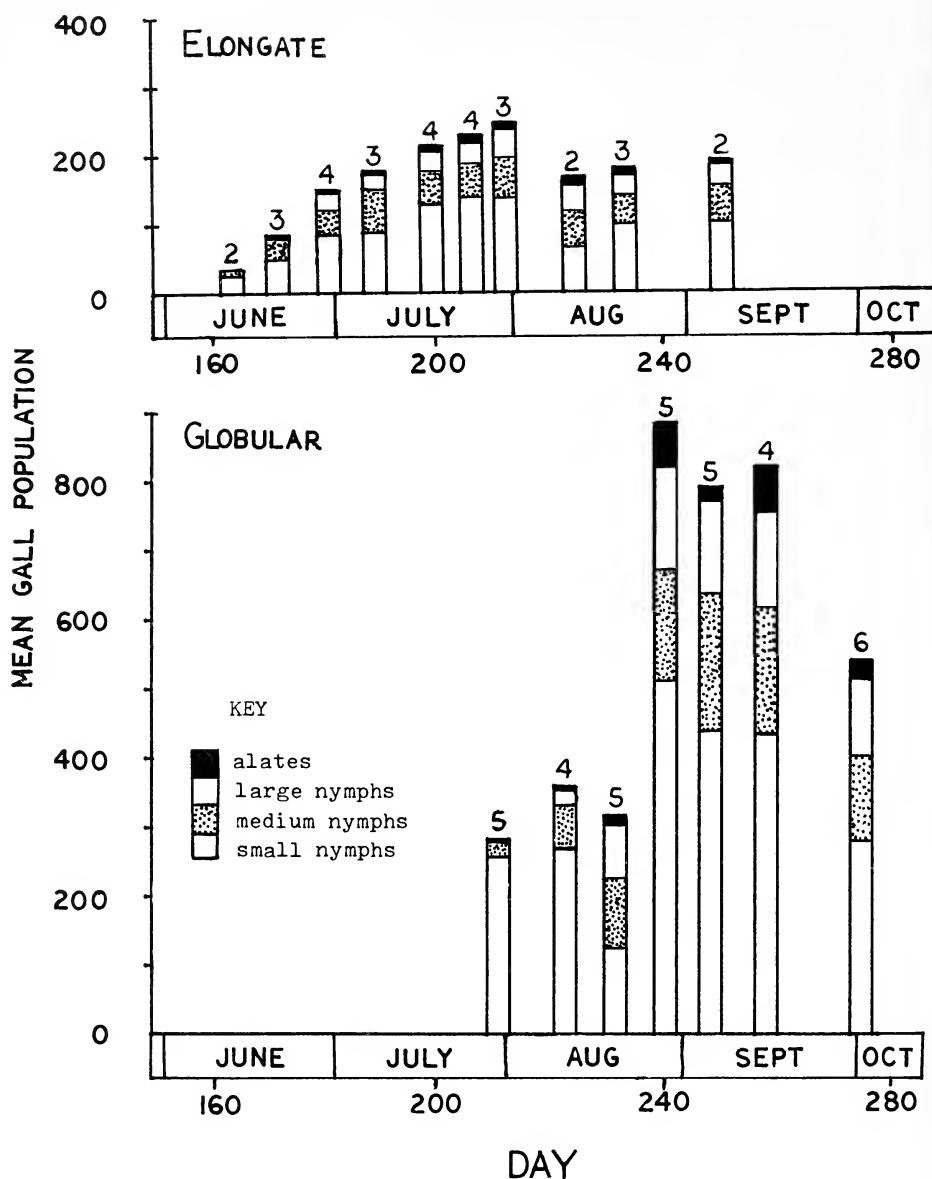


Fig. 2. Changes in mean gall population size for elongate (top) and globular (bottom) galls. Each bar is divided into segments proportional to the numbers of small, medium, and large nymphs, and alates. The sample sizes are shown above each bar. Abscissa is the same as Figure 1.

up" in maturity. The changes in the variance of the developmental stage distribution are identical in pattern. The approximately 50 day displacement of the curve for globular galls almost exactly matches the 47 day difference in time of gall *initiation* on Long Island (average of 1976, 1977 and 1978 [Faith 1979b]). The duration of the phase of low life history variance (when almost all nymphs are in the small size class) for globular galls is brief, but it is just around this time that numerous samples considered by Senner and Sokal were collected.

A more extensive investigation of the full data base of which their collections were a subset shows a seasonal pattern of life history changes very much like the one here described (Bird et al. 1979). In fact, knowledge of this pattern has enabled these authors to allocate galls of unknown status to one or the other morph.

In contrast to the *pattern* of development, the *number* of nymphs produced is very different between morphs. Peak nymph population sizes differ ($t_s = 3.23$, $P < 0.02$) with globulars reaching levels over three times as high as elongates. The seasonal progression in globular gall population size is *not* simply displaced from that of elongate galls. Because of the higher population size attained by globular galls, the numbers of small nymphs at the time of Senner and Sokal's collections are about equal to the *total* populations of the more mature elongate galls, giving the impression that small globular nymphs have accumulated without developing further.

A closer look at Figures 1 and 2 reveals some support for a much smaller scaled version of the "developmental synchrony" hypothesis in globular galls, spanning some two weeks in August instead of the whole season. In these galls the phase of rapid increase in life history variance happens without an appreciable increase in the number of nymphs in the gall, as though a large initial cohort begins to mature before many new small nymphs are produced. Elongate galls, in contrast, show a gradual rise in number of nymphs during their phase of life history variance increase.

In conclusion, an investigation of the progress of maturation of globular and elongate galls of *Pemphigus populitransversus* shows that the between-morph differences in maturity distribution of the nymphs can be ascribed largely to their different ages at any point in time. A large scale qualitative difference in the progress of maturation, such as that hypothesized by Senner and Sokal, is not found. However, some differences independent of gall age are found; these are peak population size and its rate of attainment.

Whether the life history differences between morphs can be considered to be adaptations to different circumstances is difficult to say. Certainly the existence of the globular morph enables exploitation of a new resource, namely the late flush of leaves, which seems to be unexploited by other *Pemphigus* species. Stem mothers seem to have no limit to the numbers of

nymphs they can produce. Unborn nymphs may still be found in stem mothers taken from galls on abscised leaves in the autumn. However, the fecundity of stem mothers should be influenced by genetic and environmental factors. The greater fecundity and consequent higher population size of globular galls may be a phenotypic response to maturation in the warmer climate of mid-summer or to nutritive or anatomical differences between the early and late flushes of leaves. Faith (1979a) has shown strong association of population size with measurements of the leaves both within and between morphs.

Acknowledgments

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Department of Ecology and Evolution, S.U.N.Y. at Stony Brook, Stony Brook, New York 11794.

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EPISTYLUS CAMBARI (CILIATA: PERITRICHIDA) AND
DRAGONFLY NYMPHS, AN EPIZOIC ASSOCIATION

Reid Jilek

Abstract.—*Epistylis cambari* was found attached to the dorsal abdominal surface of 30% of the dragonfly nymphs examined. Colonies ranged from 20–30 individuals with but one colony attached to each dragonfly nymph.

Introduction

Members of the genus *Epistylus* characteristically form epizoic associations (Sleigh 1975). Associations involving *Epistylus* have been recorded from crayfish (Kudo 1954), chironomid larvae (Jahn 1949), fishes (Crites 1977; Rogers 1971), and turtles (Bishop and Jahn 1941). This study has revealed the presence of *Epistylus cambari* from dragonfly nymphs.

Materials and Methods

A total of 30 dragonfly nymphs was collected from ponds 47, 48, 49, and 50 on the Delaware Reservoir Wildlife Area, Delaware County, Ohio, during April 1979. The nymphs were identified as *Gomphus quadricolor* Walsh (family Gomphidae) and *Pachydiplax longipennis* Burmeister (family Libellulidae).

The nymphs were maintained for one week in individual petri dishes filled with distilled water. After one week the nymphs were examined.

Identification of *Epistylis cambari* to species was performed following removal from the dragonfly nymphs. *E. cambari* were stained with Harris haematoxylin and Rose Bengal and examined by light microscopy.

Results

Nine of the 30 dragonfly nymphs (6 of 12 *G. quadricolor* and 3 of 18 *P. longipennis*) were found to have single colonies of *Epistylis cambari* attached to their dorsal abdominal surfaces. Each colony was comprised of 20–30 individuals. No evidence of pathology was observed at the site of attachment of *E. cambari*.

Discussion

Dragonfly nymphs provide a suitable environment for *Epistylis*. The rather sedentary existence of the nymphs allows for attachment of telotrochs and subsequent development into a colonial form. This epizoic association

is further enhanced by the hardened sclerotized abdominal plates of the dragonfly nymphs.

The presence of *E. cambari* attached to dragonfly nymphs represents a new host record. The presence is, however, not inexplicable since dragonfly nymphs commonly co-inhabit areas with crayfish, a known host of *E. cambari* and the ponds are inhabited by numerous crayfish.

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Department of Zoology and The Center for Lake Erie Area Research,
The Ohio State University, Columbus, Ohio 43210.

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TOTAL CONCENTRATION OF FREE AMINO ACIDS AND THE
CORRESPONDING MORPHOGENETIC CHANGES DURING
THE EMBRYOGENESIS OF *CHILOMENESE SEXMACULATA*
FABR. (COLEOPTERA: COCCINELLIDAE)

Devinder Mukesh, Dalbinder Singh Sidhu¹ and Nirmal Kumar

Abstract.—The concentration of free amino acid (FAA) pool in relation to the various morphogenetic events occurring during embryogenesis of *Chilomenes sexmaculata* Fabr. was determined at different incubation periods. During the first 12 hours of embryogenesis, when the zygote undergoes an active cleavage, the concentration declines gradually. However, it rises sharply at 15 hours of development when the cleavage energids undergo an active migratory activity. The amount of FAA decreases at 24 hours and remains almost steady up to 35 hours of incubation when the embryo starts elongation and segmentation. From then on there is a continuous increase in FAA up to 75 hours followed by a declining trend towards hatching as the yolk gets depleted.

Introduction

Extensive reviews on the biochemical investigations pertaining to the nitrogen metabolism during embryogenesis of insects have earlier been made by Chen (1962, 1966) and Corrigan (1970). To get a greater insight into the development of an embryo it is necessary to elucidate the relationship of biochemical changes to the corresponding morphogenetic events occurring during this period. Since the major processes underlying differentiation at the embryonic level aim at protein synthesis which in turn depends on the supply of free amino acids (FAA) from the yolk reserves, FAA thus have a distinct relationship to morphogenesis.

The present attempt unveils a relationship between the total concentration of FAA and the corresponding morphogenetic events occurring during the different incubation periods in *Chilomenes sexmaculata* Fabr.

Materials and Methods

The adults of *C. sexmaculata* were collected from the *Calotrips procera* plants during the months of November to February around Patiala (India) and were reared in the laboratory according to Sarswat (1976) on *Aphis neri*. Numerous batches of eggs were obtained, incubated at $28 \pm 2^\circ\text{C}$ for

¹ All correspondence to this author.

Table 1. Concentration of FAA pool and various morphogenetic events occurring during embryogenesis of *Chilomenes sexmaculata* Fabr.

Incubation period (hr)	μM FAA/100 eggs ($\pm\text{SD}$)*	Morphogenetic event
0.25	1.51 ± 0.030	Maturation of the male as well as female pronucleus (Fig. 1).
1.00	1.48 ± 0.029	Fusion of male and female nucleus (Fig. 2).
3.00	1.34 ± 0.027	Cleavage of the zygote, giving rise to 4-energids stage (Fig. 3).
5.00	1.46 ± 0.029	8-cleavage energids stage (Fig. 4).
7.50	1.16 ± 0.023	The process of cleavage continues.
12.00	1.11 ± 0.022	240 ± 16 energids stage (Fig. 5).
15.00	1.77 ± 0.035	Migration of the cleavage energids towards the periplasm starts (Fig. 6).
19.00	1.68 ± 0.035	A syncytial primary epithelium is formed (Fig. 7).
24.00	1.37 ± 0.028	A regular layer of primary epithelial cells observed (Fig. 8).
31.00	1.39 ± 0.028	The ventro-posterior portion of the primary epithelium becomes thickened, the cells being columnar, so as to give rise to the definitive germ primordium (ventral plate) (Fig. 9).
35.00	1.32 ± 0.026	Elongation of the germ band or ventral plate takes place and the germ band becoming faintly distinguishable into an anterior protocephalon and the posterior protocorm (Fig. 10).
45.00	1.42 ± 0.028	Further elongation of the germ band resulting in the formation of three protocormic regions (Fig. 11).
60.00	1.45 ± 0.029	The germ band becomes segmented with delineated appendages (Fig. 12).
72.00	1.48 ± 0.029	
75.00	1.55 ± 0.030	An active growth period, the appendages further develop and the process of cephalization starts, secondary yolk cleavage, yolk poly-hedra formed.
90.00	1.35 ± 0.026	The appendages become fully formed and the head also becomes distinct with the usual appendages (Fig. 13).
100.00	1.30 ± 0.026	Fully formed embryo.
110.00	1.22 ± 0.024	Hatching takes place.

* Standard deviation. Each reading is an average of three determinations.

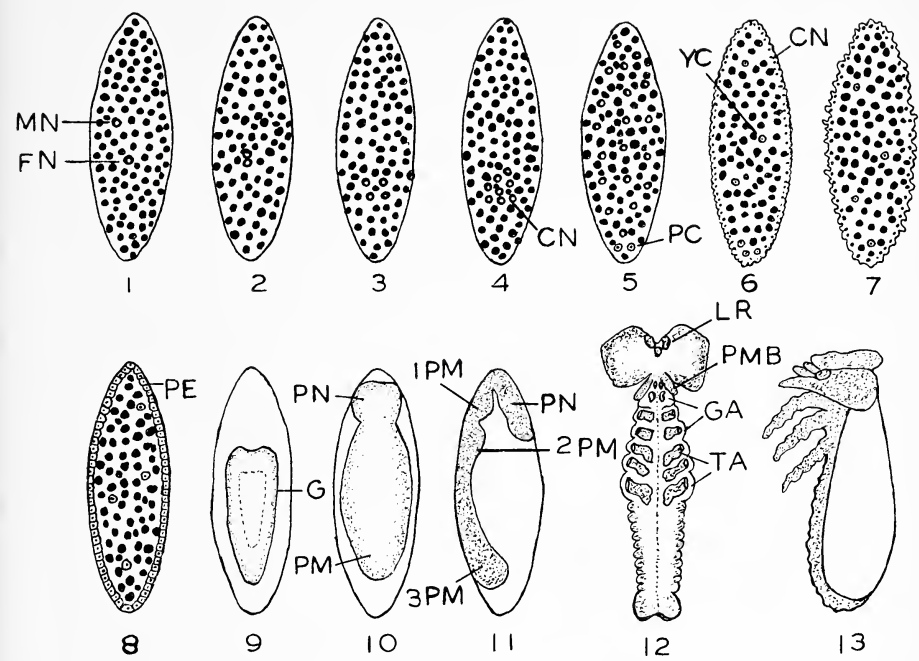


Fig. 1. Abbreviations: CN, cleavage energid; FN, female pronucleus; G, germ band; GA, gnathal appendages; LR, labral appendages; MN, male pronucleus; PC, pole cell; PE, primary epithelium; PM, protocorm; 1PM, 2PM, 3PM, 1st, 2nd and 3rd protocormic regions; PMB, premandibular appendages; PN, protocephalon; TA, thoracic appendages; YC, yolk cell.

definite periods and subsequently fixed in Carl's fixative at 60°C for 2 hours. The permanent preparations were made according to the method of Rempel and Church (1971) to observe various developmental changes in the embryo. The FAA extracts from the various egg samples at specific incubation periods were prepared according to Sidhu and Kang (1979). The quantitation of FAA pool was made by the method of Troll and Cannon (1953).

Results and Discussion

The concentration of FAA pool and the various morphogenetic events occurring during the embryogenesis of *Chilomenes sexmaculata* Fabr. are recorded in Table 1. At 0 hour, i.e., immediately after oviposition, the concentration was $1.51 \pm 0.030 \mu\text{moles}/100 \text{ eggs}$, which decreased three hours later to $1.34 \pm 0.027 \mu\text{moles}/100 \text{ eggs}$. This decrease in FAA concentration corresponds to the period when the exochorion of the newly laid egg becomes hard and

dark in color, apparently indicating the utilization of FAA in this process. It has further been noted that there is a continuous decrease in FAA concentration up to 12 hours of incubation, i.e., during the active cleavage activity when the zygote nucleus undergoes multiple synchronous divisions. This decrease suggests that the breakdown of yolk proteins has not yet started and the need of amino acids for protein synthesis is met from the already existing FAA pool accumulated during maturation of egg. The initiation of protein synthesis immediately after fertilization has earlier been reported by Lockshin (1966) in some coleopterous insects.

At about 15 hours of incubation, when energids start migrating, the concentration of FAA suddenly increases to a fairly high value (1.77 ± 0.035 μ moles/100 egg). This increase is due perhaps to the lysis of yolk proteins, with the result that the mixing-up of the yolk contents facilitates the peripheral migration of the cleavage energids. This type of increase in FAA concentration has been observed by Chen and Briegel (1965) in *Culex pipens morestus* at a stage when blastoderm formation and elongation of germ band (Idris 1960) takes place.

The FAA concentration sharply decreases (1.37 ± 0.28 μ moles/100 eggs) at 24 hours of incubation when a regular primary epithelial layer gets established, revealing a higher rate of protein synthesis in comparison with the breakdown of yolk proteins. Thereafter the concentration remains almost steady up to 34 hours of development. During this period the differentiation of the ventral plate or the germ band is completed.

At 45 hours of development the amount of FAA again rises (1.42 ± 0.028 μ moles/100 eggs), when the germ band undergoes further elongation and primary segmentation. This trend in FAA concentration increase was observed in the following 30 hours of development. The peak is reached at 75 hours of incubation when the embryo shows an active development. This increase in concentration can be attributed to an active lysis of the yolk proteins, corresponding to an active growth period when cephalization as well as the phenomenon of secondary yolk cleavage takes place.

After this period, the FAA concentration shows a continuous decline when the appendages become fully formed and the head becomes quite distinct. This decline in concentration prior to hatching is due perhaps to the fact that the yolk reserves become increasingly exhausted at this stage and the supply of amino acids can no longer keep pace with the demand for more amino acids for protein synthesis. Chen (1966) and Indira (1963) have also observed a similar type of decrease in FAA concentration towards hatching.

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Department of Zoology, Punjabi University, Patiala-147002, India.

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A CONSPECTUS OF PENTATOMINI GENERA OF THE WESTERN
HEMISPHERE. PART I (HEMIPTERA: PENTATOMIDAE)

L. H. Rolston, F. J. D. McDonald and Donald B. Thomas, Jr.

Abstract.—The Pentatomini of the Western Hemisphere is divided into 3 sections. Keys are provided to separate these sections and the genera of one section, viz. those genera that have a median tubercle at the base of the abdominal venter and a metasternal production apposing this tubercle. Four new monotypic genera are diagnosed, each based on a new species: *Elanela hevera* Rolston, n. sp., *Glaucioides englemanni* Thomas, n. sp., *Nocheta adda* Rolston n. sp. and *Vidada dollingi* Rolston n. sp. The genus *Phineus* Stål is removed from this group and placed in Discocephalinae.

There is no conspectus of Western Hemisphere genera of Pentatomini more recent than the work of Stål (1867). Stål's conspectus is now inadequate because of the many genera subsequently added to the tribe.

As a foundation for this conspectus we have previously provided keys and diagnoses for the Western Hemisphere families of pentatomoids, subfamilies of pentatomids and tribes of the nominate subfamily (Rolston and McDonald 1979).

The present work divides the Pentatomini into three sections, which separate rather clearly with the exception of sexually dimorphic species of the genus *Dendrocoris*, and provides a key to the genera of section 3. Genera of this section have on the third abdominal sternite (second visible) a median tubercle that is apposed by the posterior margin of the metasternum. The metasternum is produced ventrad, at least posteriorly, and often interlocks with the abdominal spine.

The genus *Bathycoelia*, most species of which are African, is included in this section since 2 species of the genus were described from specimens supposedly collected in South America (Jensen-Haarup 1931 and 1937). These specimens were examined and they do indeed belong in *Bathycoelia*. Although the presence of this genus in South America is not unthinkable, its existence there needs confirmation.

The genus *Phineus* Stål, which has customarily been placed among the genera of section 3, is transferred to Discocephalinae on the basis of rostral and trichobothrial characters (Rolston and McDonald 1979).

Key to Sections of Pentatomini

1. Abdominal venter bearing median tubercle or spine at base

- Base of abdominal venter smooth medially, not clearly produced
Section 1
- 2. Metasternum projecting ventrad (at least between metacoxae) with posterior margin in apposition to median tubercle on base of abdominal venter (Fig. 23)
Section 3
- Median tubercle or spine at base of abdominal venter free distally, not in apposition to posterior margin of metasternum (Fig. 24)
Section 2

Key to the Western Hemisphere Genera of Pentatomini

Key to Genera of Pentatomini, Section 3

1. At least hind femora with two rows of spines on inferior surface (Fig. 1); body depressed *Placocoris* Mayr
 - Inferior surface of femora unarmed; body normally convex 2
2. Rostrum lying in deep mesial groove extending almost or entirely length of abdominal venter *Bathycoelia* Amyot & Serville
 - Abdominal venter not grooved mesially or only shallowly so basally 3
3. Tarsi 2-segmented *Phalaecus* Stål
 - Tarsi 3-segmented 4
4. Superior surface of at least mesothoracic femora prolonged distally as small spine (Fig. 2) 5
 - Superior surface of femora unarmed distally 7
5. First rostral segment lying entirely between bucculae; ostiolar rugae reaching more than halfway from inner margin of ostioles to lateral margin of metapleura (Fig. 3) *Pallantia* Stål
 - First rostral segment projecting beyond bucculae; ostiolar rugae reaching less than halfway from inner margin of ostioles to lateral margin of metapleura (Fig. 4) 6
6. Juga surpassing tylus, acute apically; superior surface of tibiae sulcate *Arvelius* Spinola
 - Juga not surpassing tylus; superior surface of tibiae rounded except distally *Taurocerus* Amyot & Serville
7. Metasternum bifurcate anteriorly and extending onto swollen mesosternum (Fig. 5) 8
 - Metasternum usually entire anteriorly, occasionally with pair of carinae 10
8. Anterolateral margins of pronotum fimbriate; ostiolar rugae extending halfway from mesial margin of ostioles to lateral margin of metapleura *Neopharnus* Van Duzee
 - Anterolateral margins of pronotum entire; ostiolar rugae extending

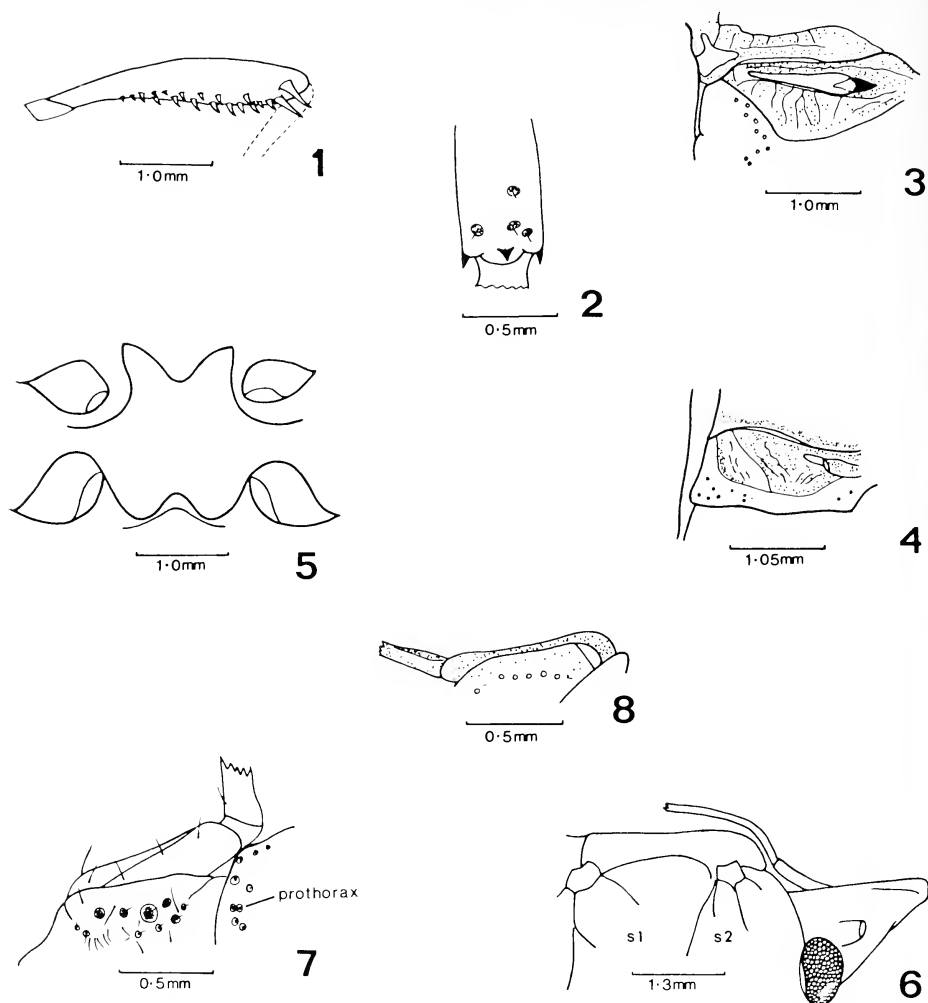
- about 3 fourths of distance from inner margin of ostioles to lateral margin of metapleura 9
9. Rostrum extending well beyond abdominal sternite bearing tubercle *Pharnus* Stål
- Rostrum extending little or not at all past metacoxae *Praepharnus* Barber & Bruner
10. Mesosternal carina projecting cephalad between procoxae and beyond anterior limits of procoxae (Fig. 6) 11
- Mesosternal carina if projecting cephalad terminating between procoxae 12
11. Apex of scutellum emarginate; ostiolar rugae nearly reaching lateral margin of metapleura *Evoplitus* Amyot & Serville
- Apex of scutellum entire; ostiolar rugae extending about 2 thirds of distance from inner margin of ostiole to lateral margin of metapleura *Pseudevoplitus* Ruckes
12. Ostiolar rugae reaching more than halfway from inner margin of ostioles to lateral margin of metapleura 20
- Ostiolar rugae reaching less than halfway from inner margin of ostioles to lateral margin of metapleura 13
13. Distal end of first rostral segment clearly projecting beyond bucculae (Figs. 7, 8) 14
- Distal end of first rostral segment not or scarcely projecting beyond bucculae 18
14. Ratio of head width across eyes to length of head 10:8–10:10 15
- Ratio of head width across eyes to length of head 10:7 or less 16
15. Humeral angles conspicuously produced; rostrum reaching mesocoxae *Myota* Spinola
- Humeral angles little produced; rostrum reaching metacoxae *Vidada* Rolston, new genus
16. Metasternum saddle-shaped, transversely depressed between metacoxae and mesocoxae (in part) *Brachystethus* Laporte
- Metasternal production nearly flat or obtusely carinate 17
17. Rostrum reaching mesocoxae; antennal segment 2 much shorter than 3 *Lopadusa* Stål
- Rostrum reaching metacoxae; antennal segment 2 much longer than 3 *Elanela* Rolston, new genus
18. Metasternal production nearly flat *Serdia* Stål
- Metasternal production sloping or arched 19
19. Metasternal production greatest posteriorly, sloping dorsad anteriorly, weakly carinate anteriorly *Marghita* Ruckes
- Metasternal production longitudinally arched, carinate for entire length *Stictochilus* Bergroth

20. Distal end of first antennal segment clearly surpassing apex of head 21
 - Distal end of first antennal segment not or scarcely surpassing apex of head 24
21. Metasternum much more produced than mesosternum, often bulbous (Fig. 9) (in part) *Brachystethus* Laporte
 - Metasternal production flattened or obtusely carinate, together with abdominal spine and mesosternal carina forming nearly continuous profile (Fig. 10) 22
22. Metasternal production flattened; distal end of first rostral segment surpassing bucculae 23
 - Metasternal production obtusely carinate; distal end of first rostral segment not or scarcely surpassing bucculae *Paratibilis* Ruckes
23. Mesosternal carina forming thin wedge between procoxae, projecting slightly onto prosternum (Fig. 11) *Tibilis* Stål
 - Mesosternal carina little elevated, not projecting beyond mesosternum (in part) *Janeirona* Distant
24. Interocular distance more than twice width of one eye; juga well separated apically 25
 - Interocular distance less than twice width of one eye; juga contiguous or nearly so apically *Nocheta* Rolston, new genus
25. Distal end of first rostral segment clearly exceeding bucculae 26
 - First rostral segment lying entirely between bucculae 27
26. Apex of rostrum extending to or beyond posterior margin of third sternite; juga no longer than tylus *Pharypia* Stål
 - Apex of rostrum not projecting beyond metacoxae; juga surpassing tylus (in part) *Janeirona* Distant
27. Posterior margin of metasternum excavated medially and apex of abdominal spine fitting into this excavation (Fig. 14) *Glaucioides* Thomas, new genus
 - Posterior margin entire medially or with shallow subvertical sulcus *Banasa* Stål

Elanela Rolston, new genus

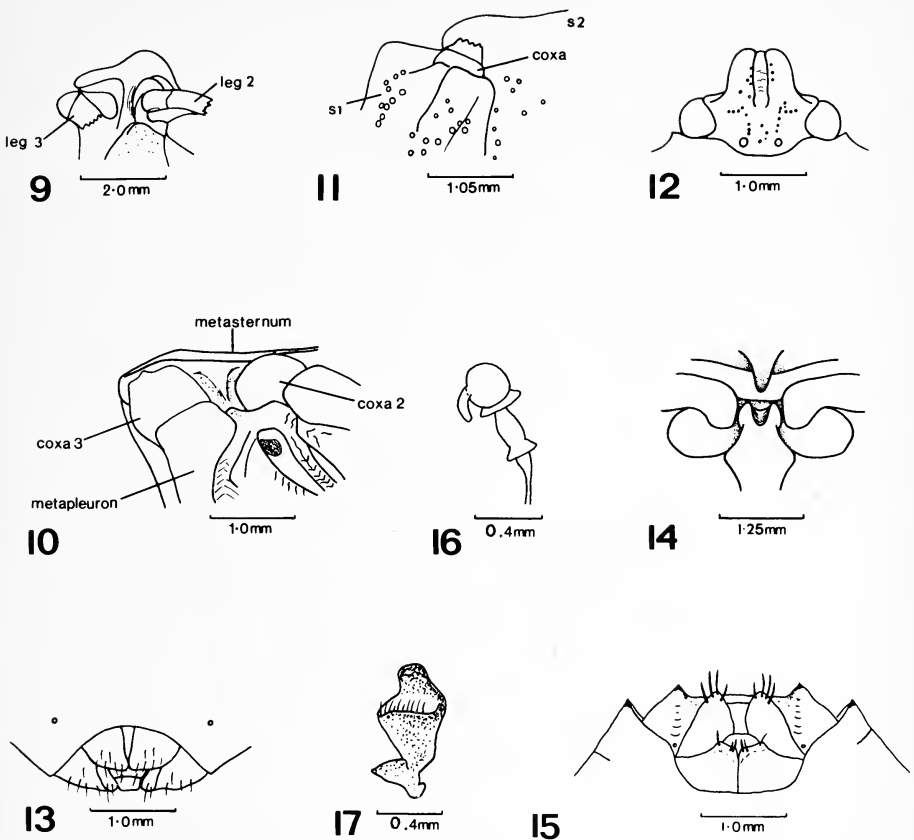
Type species.—*Elanela hevera* Rolston, n. sp.

Diagnosis.—Median tubercle of abdominal sternite 3 (second visible) fitting into notch in posterior margin of metasternum. Metasternum produced, flat and bifurcate posteriorly, becoming obtusely carinate anteriorly. Mesosternum obtusely carinate mesially, forming continuous profile along meson with metasternum, anteriorly apposing two low carinae on prosternum which diverge and continue as anterior prosternal margin. Ostiolar ruga on



Figs. 1-8. 1. *Placocoris viridis*—right hind femur. 2, 3. *Pallantia macula*—2. Left mid femur, apex. 3. Right metathoracic scent gland. 4. *Arvelius latus*—right metathoracic scent gland. 5. *Pharnus inconspicuus*—metasternum. 6. *Pseudevoplilus longicornis*—mesosternal carina, lateral. 7. *Lopadusa augur*—right buccula, lateral. 8. *Elaneta hevera*—left buccula, lateral. (S1, S2), sternites one, two.

each metapleuron extending between 1 fourth and 1 half of distance from mesial margin of ostiole to lateral margin of metapleuron. Femora unarmed; tibiae sulcate; tarsi 3-segmented. Bucculae posteriorly curving to surface of head. Basal segment of rostrum projecting past bucculae (Fig. 8); apex of rostrum reaching metacoxae. Length of head about 6 tenths of width across eyes. Jugal and tylus subequal in length; lateral margins of jugal deeply con-



Figs. 9–17. 9. *Brachystethus rubromaculatus*—meso-, metasterna, lateral. 10. *Janeirona bergi*—meso-, metasterna, lateral. 11. *Tibilis parva*—pro-, mesosterna, lateral. 12. *Elanela hevera*—head, dorsal. 13. *Elanela hevera*—female genitalia. 14–17. *Glaucioides englemani*. 14. Metasternum, ventral. 15. Female genitalia. 16. Spermatheca. 17. Left paramere. (S1, S2), sternites one, two.

cave before eyes (Fig. 12). Basal segment of antennae stout, reaching to or slightly beyond apex of head.

Elanela hevera Rolston, n. sp.

Stramineous with castaneous to black punctures and markings. Length 7.5 mm, width at humeri 4.5 mm.

Head sparsely punctate excepting line of contiguous punctures on each side touching ocellus mesially and curving anteriorly then laterally toward middle of eye. Lateral margin of juga parallel between anterior convexity and concavity before eyes, narrowly bordered in brown. Width of head

across eyes 1.9 mm, length 1.2 mm; interocular width about 1.05 mm; width across ocelli about 0.65 mm. Antennal segments 0.4, 1.0, 0.8, 1.5, 1.7 mm long; distal half of segments 4 and 5 black. Rostral segments 2 through 4 about 1.0, 0.7, 0.5 mm long; distal end of segment 2 at middle of mesosternum, of segment 3 at mesocoxae, of segment 4 at metacoxae.

Pronotal punctures arranged in line on anterior and anterolateral submargins, along posterior boundary of cicatrices and posterior boundary of narrow transverse callus lying immediately caudad of cicatrices; much smaller punctures border posterior pronotal margin; a few small punctures interspersed with many larger punctures scattered over pronotal disk. Anterolateral margins straight, narrowly ridged at edge. Humeri not produced. Pronotal width at humeri 4.4 mm, length at meson 1.7 mm.

Scutellar punctations sparse on basal disk, dense elsewhere excepting impunctate apex; large stramineous callus present in each basal angle; fovea small, inconspicuous; basal width and length each 3.0 mm. Large stramineous spot on disk of each corium located in an elongate impunctate area; punctation elsewhere similar in density and strength to that on lateral portions of scutellum. Connexivum broadly exposed, black to castaneous with 2 pale macules on each segment, one arching mesad from lateral margin, one arching cephalad from posterior margin, these much reduced on first visible segment, confluent on last segment; dark areas densely punctate, light areas nearly impunctate.

Venter sparsely irregularly punctate, most strongly so on propleura. Evaporative area matte, minutely granular, without fine rugae, castaneous. Spiracles on sternite 2 exposed; peritremes dark. Posterolateral angles of sternites (except second) produced as small black spines.

Genital plates as in Figure 13.

Holotype.—Female, labeled (a) "Peru: Iquitos, 100 mi. n.e., on Napo R." (b) "Mar. 20, 1969. B. K. Dozier." Deposited in Florida State Collection of Arthropods (Gainesville, Florida). No paratypes.

Glaucioides Thomas, new genus

Type species.—*Glaucioides englemani* Thomas, n. sp.

Diagnosis.—Abdominal sternite 3 (second visible) bearing anteriorly directed spinose tubercle, this tubercle received by elongated socket on posterior surface of metasternum. Socket slanting anteroventrad, closed ventrally (open in related genera) (Fig. 14). Metasternum pubescent, mildly convex, elevated posteriorly, sloping and subelevated anteriorly. Low flat mesial carina on mesosternum broadened anteriorly, obsolescent on posterior $\frac{1}{4}$.

Apex of scutellum angulate, not bluntly rounded as in related genera.

Ostiolar rugae sinuate, elongate, extending nearly to the edge of metapleura. Femora unarmed; tibia terete; tarsi 3-segmented.

Basal segment of rostrum lying entirely within bucculae, latter evanescent posteriorly. Jugae and tylus subequal in length. Basal segment of antennae not surpassing apex of head.

Etymology.—Named to reflect morphological similarity to the Indo-Malaysian genus *Glaucias* Kirkaldy 1908.

Glaucoides englemani Thomas, n. sp.

Stramineous, devoid of darkened punctures; abdominal tergites and sometimes jugae, pronotum and connexivum thinly margined with red; acuminate tips of connexival angles black. Weak punctures densest on pronotum and apical $\frac{1}{3}$ of scutellum; head without or only feebly punctate; dorsal surface strigose at bases of jugae.

Head width across the eyes 2.1 mm, length 2.2 mm; interocular width 1.3 mm. Antennal segments: 0.51, 0.75, 1.25, 1.50, 1.51 mm long; distal $\frac{1}{2}$ of segments 3 and 5, and nearly all of segment 4 dark brown. Rostral segments 2 through 4: 1.1, 1.0, 0.8 mm long, tip of rostrum just attaining abdominal tubercle.

Anterolateral pronotal margins straight, obtuse; humeri not produced; cicatrices inconspicuous. Pronotal width 5.6 mm, length at meson 2.5 mm.

Basal disk of scutellum mildly convex and more sparsely punctate than apex. Apex of scutellum angulate, pointed; length 4.0 mm. Hemelytra with weak, dense punctures, nearly translucent; membrane hyaline.

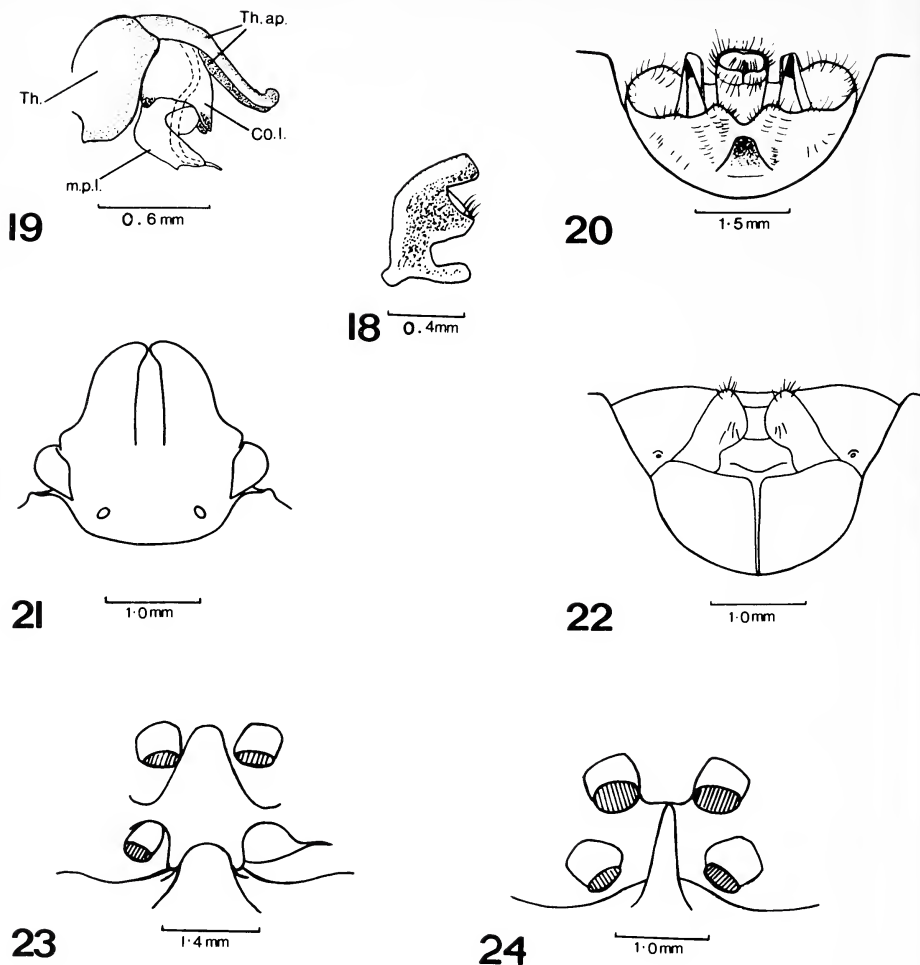
Venter of abdomen broadly V-shaped in cross section, sloping sides flat, impunctate. Peritremes of spiracles concolorous with venter.

Tergite 6 of female bearing a pair of triangulate, posteriorly directed teeth (Fig. 15). Spermathecal bulb with a lateral process (Fig. 16). Pygophore of male open, ventral border broadly V-shaped from caudal view; inferior margin broadly, shallowly emarginate, subtended by a broad, shallow sulcus which becomes obsolescent laterally. Pygophore otherwise unelaborated. Proctiger broad, dorsal aspect trapezoidal, with a shallow, transverse, mesial depression. Parameres squat, goblet shaped, with a broad spatulate apophysis extending from rim of its bowl (Figs. 17, 18). Aedeagus with a pair of elongate thecal processes (Fig. 19).

Length.—♂ 10.1 mm, ♀ 11.3 mm. Width: ♂ 5.6 mm, ♀ 6.3 mm.

Etymology.—This species is named for H. Dodge Engleman, M.D., of Coco Solo, Panama, who has presented us with numerous specimens of Pentatomidae for study, including one of the types upon which this species is based.

Holotype.—♂ Sinop, Brazil, (Mato Grosso): Lat. 12°31', Long. 55°37'.



Figs. 18–24. 18, 19. *Glaucioides englemani*. 18. Left paramere, lateral. 19. Aedeagus. 20. *Nocheta adda*—genital cup. Figs. 21, 22. *Vidada dollingi*. 21. Head, dorsal. 22. Female genitalia. 23. *Serdia concolor*—metasternum. 24. *Ramosiana insignis*—metasternum. (Co. l.), conjunctival lobe, (m. p. l.), median penial lobe, (Th.), theca, (Th. ap.), thecal appendage.

Oct. 1974. M. Alvarenga Collr. Deposited in the American Museum of Natural History.

Paratypes.—3♂♂ same locality, date and collr; 1♂ same locality and collr., Oct. 1975; 1♂ Barro Colorado Island, Panama, 5 May 1937, S. W. Frost collr; 1♀ Barro Colorado Island, Panama, 1–9 May 1964, W. D. and S. S. Duckworth collrs; 1♂ Barro Colorado Islan, Panama, 1 May 1973, D. Engleman collr; 1♀ Mepane Kamp, Surinam, Aug. 1961, J. P. Shulz

collr; 1♀ Mt. Duida, Venezuela, 25 Feb. 1924, unk. collr; 1♀ Kuyuwini River, British Guiana, 22 Nov. 1937, W. G. Hassler collr. Deposited in the collections of the American Museum of Natural History, U.S. National Museum, California Academy of Sciences and the authors.

Nocheta Rolston, new genus

Type species.—*Nocheta adda* Rolston, n. sp.

Diagnosis.—Median tubercle on abdominal sternite 3 (second visible) fitting into notch in posterior margin of metasternum. Metasternum produced, surface flat with lateral ramus on each side between meso- and metacoxae, apposed anteriorly by mesosternal carina. Mesosternum tumescent; mesial carina broad basally and continuing profile of metasternum when viewed laterally, narrowing anteriorly to acuminate termination between procoxae. Arms of chevron shaped production on prosternum diverging cephalad of procoxae, continuing along anterior submargin of proplura, terminating behind eyes. Ostiolar sulcus and ruga on each side reaching about 8 tenths of distance from mesial margin of ostiole to lateral margin of metapleuron. Femora unarmed; tibiae sulcate; tarsi 3-segmented. Bucculae evanescent posteriorly. First rostral segment lying entirely between bucculae. Juga convergent before tylus; lateral margin of juga deeply concave before eyes. Basal segment of antennae scarcely projecting past apex of head.

Nocheta adda Rolston, n. sp.

Stramineous with dark castaneous to black punctation and markings. Length about 9.1 mm, width at humeri 5.2 mm.

Line of dense punctation along both margins of tylus continuing over vertex, converging at base of head; mesial margin and longitudinal band on disk of juga densely punctate; punctures about eye irregularly disposed. Lateral jugal margins sigmoid, nowhere parallel, narrowly bordered in black. Width of head across eyes 2.5 mm, length 1.5 mm; interocular distance 1.2 mm; distance across ocelli about 0.85 mm. Ocelli rather larger, about 0.2 mm in diameter. Antennal segments 0.5, 1.5, 1.6, 2.2, 2.1 mm long; color stramineous to fulvous, first 3 segments darkly dotted, third faintly so, fifth fuscous on distal half. Rostral segments 2 through 4 about 0.8, 0.9, 0.5 mm long; segment 2 reaching procoxae; apex of segment 4 nearly attaining mesocoxae.

Narrow pale callus traversing pronotum along posterior margins of cicatrices. Row of closely spaced punctures surrounding cicatrices, a few punctures scattered on cicatrices. Anterolateral margins straight with single row of punctures between narrowly reflexed margin and submarginal impunctate band. Punctation elsewhere on pronotum mostly in transverse lines, these

longer and somewhat vermiform basally. Humeri not produced. Pronotal width 5.2 mm, length at meson 2.2 mm.

Scutellar punctations in transverse vermiform castaneous bands; basal angles without callus or fovea; width at base 3.5 mm, length 4.0 mm; frena extending along basal 6 tenths; apex acute. Coria blotched with castaneous; punctation stronger than on scutellum; membrane fumose with about a dozen simple veins. Connexiva moderately exposed, alternately banded where exposed with dark border on each side of intersegmental sutures.

Venter sparsely and weakly punctate excepting moderately dense punctation on propleura. Evaporative areas matte, not rugulose, concolorous with remainder of meso- and metapleura. Spiracular peritremes concolorous with surrounding area of sternites.

Posterior surface of pygophore with deep mesial triangular impression below emargination of dorsal border; subacute tooth present on each side of emargination. Parameres acicular, partially obscuring subvertical ridge on anterior wall of genital cup (Fig. 20).

Holotype.—Male labeled (a) "Hyutanahan Rio Purus Brazil. S. M. Klages." (b) "March 1922." Deposited in U.S. National Museum. Type no. 72138. No paratypes.

Vidada Rolston, new genus

Type species.—*Vidada dollingi* Rolston, n. sp.

Diagnosis.—Metasternal production almost flat, posterior margin lightly notched mesially, anterior margin truncate and slightly less produced than adjacent part of mesosternum. Mesosternal carina broad, flattened between mesocoxae and procoxae, compressed between procoxae, not extending onto prosternum. Prosternum tumescent with low carina on each side curving anterolaterad from between procoxae. Ostiolar ruga on each metapleuron extending about 3 tenths of distance from mesial margin of ostiole to lateral margin of metapleuron. Femora unarmed; tibiae sulcate; tarsi 3-segmented. Bucculae sloping caudad to surface of head. Basal segment of rostrum projecting beyond bucculae; apex of rostrum reaching mesial tubercle on abdominal venter. Length of head about 8.5 tenths of width across eyes. Juga contiguous before tylus, their lateral margins moderately concave before small obtuse anteocular process (Fig. 21). Basal segment of antennae projecting little beyond apex of head.

Vidada dollingi Rolston, n. sp.

Dorsum castaneous becoming fuscous on pronotum anteriorly and disk of head; venter dark castaneous; appendages light castaneous excepting antennal segment 3 distally and 4 fuscous. Length about 12.3 mm, width across humeri 5.9 mm.

Head flat above, jugal margins reflexed; punctation dense, somewhat rugose. Eyes appearing small relative to head width; width of head across eyes 2.35 mm, length 1.9 mm; interocular width 1.5 mm; distance across ocelli 1.1 mm. Length of antennal segments 0.8, 0.5, 1.1, 1.4 mm (last missing). Rostral segments 2 through 4 about 1.6, 1.5, 1.0 mm long.

Anterolateral margins of pronotum reflexed, slightly sinuous. Punctation dense, all of disk behind cicatrices somewhat rugose. Width at humeri 5.9 mm, length at meson 2.6 mm.

Scutellum less densely punctate but basally more rugose than pronotum; fovea in basal angles deep; basal width 3.6 mm, length 4.7 mm; frena extending along basal 6 tenths of scutellum. Coria punctate similarly to pronotum, immaculate; membrane darkly fumose with about 7 weak simple veins. Connexiva almost unicolorous, modestly exposed.

Thoracic venter strongly and densely punctate; abdominal venter weakly but densely punctate laterally, becoming almost impunctate mesially. Evaporative area strongly rugose, punctate. Spiracles small, oval, with black peritreme.

Genital plates as in Figure 22; surface of 9th paratergite convex, strongly so basally.

Holotype.—Female, labeled (a) "Machu-Picchu, Cuzco. 8-V-65" (b) "arbusto" (c) "1067" (d) "CUZCO." Deposited in Museu Nacional, Rio de Janeiro, Brazil.

No paratypes.

Comments.—This species is dedicated to W. R. Dolling, of the British Museum (Natural History), whose unstinting assistance to fellow hemipterists is indispensable.

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(LHR) Department of Entomology, Louisiana Agricultural Experiment Station, Louisiana State University, Baton Rouge, Louisiana 70803; (FJDM) Department of Plant Pathology and Agricultural Entomology, University of Sydney, Sydney, N.S.W., Australia 2006 and (DBT) Department of Entomology, University of Missouri, Columbia, Missouri 65211.

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ANATOMY OF THE MALE REPRODUCTIVE SYSTEMS OF THE
ADULTS AND PUPAE OF TWO DORYLINE ANTS,
DORYLUS (ANOMMA) WILVERTHI EMERY AND
D. (A.) NIGRICANS ILLIGER^{1,2}

Francis C. Ford³ and James Forbes

Abstract.—This is the first study of the anatomy of the male reproductive systems of the adults and pupae of the doryline ants, *Dorylus (Anomma) wilverthi* and *D. (A.) nigricans* Illiger. The external genitalia and the terminal gastric sterna are included. The reproductive systems consist of the testes and vasa efferentia, the vasa deferentia, the seminal vesicles, the accessory glands, the bound accessory gland duct, the ejaculatory duct and wedge, the aedeagal bladder, and the external genitalia. The external genitalia of these ants are composed of a basal ring and three pairs of valves, the outer, the middle, and the inner, typical of the formicid pattern. The male systems in these two species are similar in their shapes and the arrangement of the organs. Although the testes in the *nigricans* adult are absent, in the pupa there are 50-55 follicles in each testis. *Wilverthi* has 35-40 testicular follicles in both the adult and pupa. The valves of the external genitalia and terminal gastric sterna of these two species show no individual variations, other than size, in their shapes. Male systems have been described for only three other doryline ants, the Old World *Dorylus labiatus*, the New World *Eciton hamatum* and *Neivamyrmex harrisi*. This system is compared in these dorylines. Important differences exist between the male reproductive systems of the two African *Dorylus* species herein studied and the two New World dorylines previously reported. The *Dorylus* species have a larger number of testicular follicles, the shapes of their accessory glands are different, the basal ring of the genitalia is fused to the outer valves, a membrane joins the ventral margins of the inner genitalic valves, and the shapes of the genitalic valves and the subgenital plate are different.

This paper presents the first description of the anatomy of the male reproductive systems of the adults and pupae of two Old World dorylines, *Dorylus (Anomma) wilverthi* Emery and *Dorylus (Anomma) nigricans* Il-

¹ Hymenoptera: Formicidae.

² Part of the Ph.D. dissertation of the first author at the Department of Biological Sciences, Fordham University.

³ Present address: Department of Biology, Bronx Community College, CUNY, Bronx, N.Y. 10453.

liger. Descriptions of the genitalic valves and the terminal gastric sterna are also included. Male systems have been described for only three other doryline ants, the Old World *Dorylus labiatus* (Mukerjee 1926), the New World *Eciton hamatum* (Forbes 1958) and *Neivamyrmex harrisi* (Forbes and Do-Van Quy 1965). This system will be compared in these dorylines.

Seven to nine specimens each of the adults and the pupae were kindly furnished by Albert Raignier, S.J. of Belgium, who collected these ants in the Republic of the Congo, Africa, now designated Zaire, during June of 1956 and November of 1957. The pupae were advanced in development. The entire reproductive systems were dissected from the gasters of the adults and pupae, stained with borax carmine, and prepared as whole mounts for study. The external genitalia and terminal segments were also removed and mounted for study. Illustrations were prepared with the aid of a B and L trisimplex microprojector.

The reproductive systems consist of the testes and vasa efferentia, the vasa deferentia, the seminal vesicles, the accessory glands, the bound accessory gland duct, the ejaculatory duct and wedge, the aedeagal bladder, and the external genitalia (Figs. 1-3). Throughout the following descriptions, the adult system of *wilverthi* will be described first, followed by differences in the pupal system. Comparisons will then be made with the adult and pupa of *nigricans*.

The testes of *wilverthi* are located in the dorsal median region of the gaster and extend through the 2nd and 3rd gastric segments above the ventriculus (Fig. 1). The posterior portion of each testis overlies most of the seminal vesicles. Each testis is composed of about 35-40 slender, thin-walled testicular tubules that are about 8 mm in length. Each tubule ends in a narrow duct, a vas efferens. The number and the arrangement of the testicular tubules in the pupa of *wilverthi* are similar to those of the adult. In the adult of *nigricans* the testes and vasa efferentia are absent. However, in the pupa each testis consists of 50-55 tubules, and it is similar in its shape and position to that of *wilverthi*. The testes of these two species are not covered with connective tissue sheaths or capsules.

The vasa efferentia join to form a short duct, the vas deferens. Where the vasa efferentia unite, the vas deferens is slightly more dilated than it is distally. The distal portion enters the expanded seminal vesicle just below its anterior end. The vas deferens is absent in the adult of *nigricans* but present in the pupae of *wilverthi* and *nigricans*.

The seminal vesicles are large, prominent, thick-walled, U-shaped tubes that lie in the 3rd and 4th gastric segments (Fig. 1). The first part of the proximal arm lies at right angles to the direction of the testicular tubules. It continues forward and ventrolaterally, then bends sharply posteromedial toward the posterior region of the ventriculus. The proximal arm is slightly shorter than the distal, but both arms are nearly equal in diameter. The

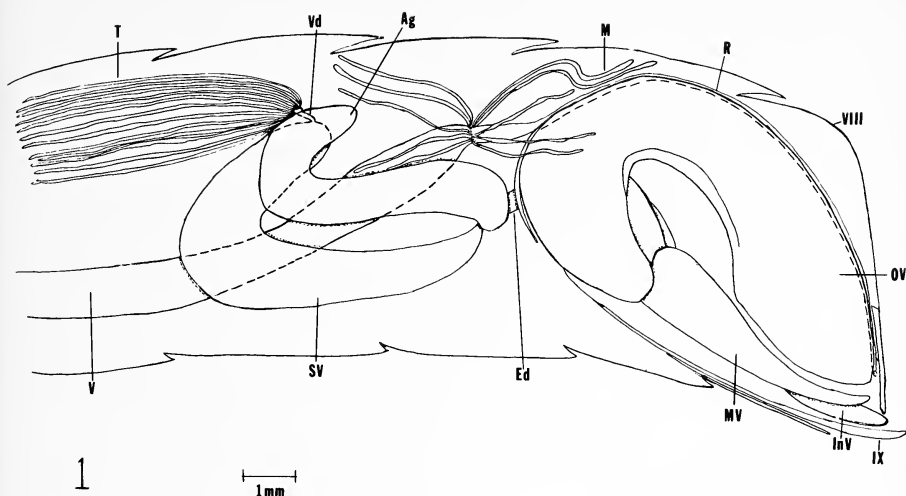
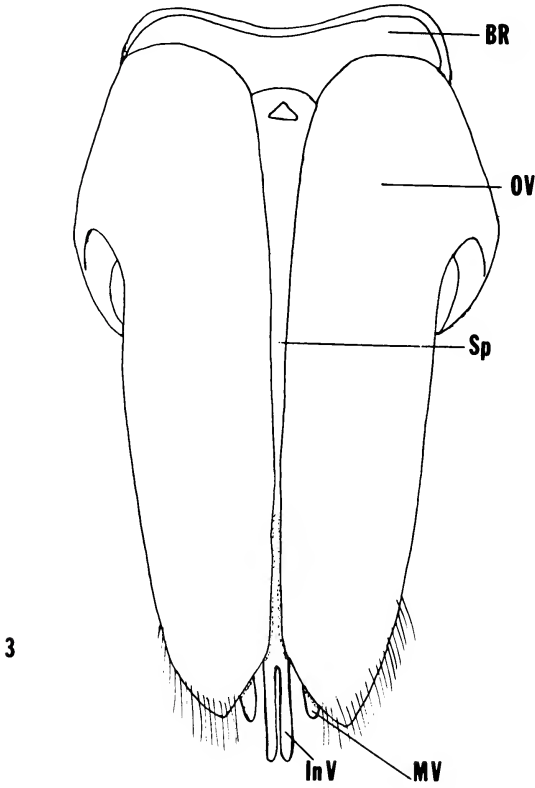
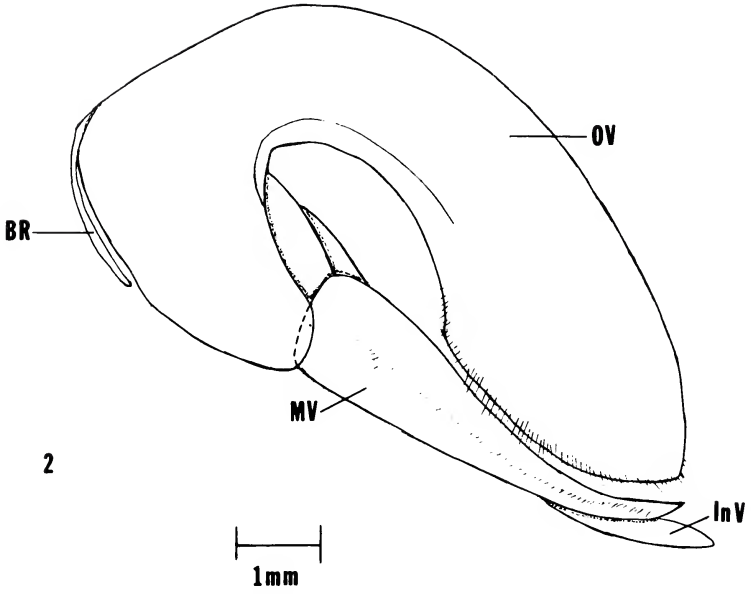


Fig. 1. Diagram of a lateral dissection of the posterior portion of the gaster of the adult male ant *Dorylus (Anomma) wilverthi*. Abbreviations: Ag, accessory gland; Ed, ejaculatory duct; InV, inner valve; M, Malpighian tubule; MV, middle valve; OV, outer valve; R, rectum; SV, seminal vesicle; T, testis; V, ventriculus; Vd, vas deferens; VIII–IX, Roman numerals designate abdominal segments.

position and arrangement of the seminal vesicles in the pupa of *wilverthi* and in the adult and pupa of *nigricans* are similar to that in the adult of *wilverthi*. Differences in the diameters of these organs between the adults of *wilverthi*, the larger species, and *nigricans* are about 25–30 percent. Likewise in both species, the diameters of the seminal vesicles of the pupae are about $\frac{1}{4}$ to $\frac{1}{3}$ smaller than those of the adults. The seminal vesicles of the *nigricans* adults were packed with sperm, while those of *wilverthi* had sperm scattered throughout. No sperm is present in these organs in the pupae. Toward the posterior margin of the 4th gastric segment each seminal vesicle tapers gradually, bends dorsomedially, and joins the accessory gland on its ventromedian surface.

Each accessory gland is a prominent, thick-walled, S-shaped tube lying above the seminal vesicles, and located on either side of the posterior region of the ventriculus (Fig. 1). Their free ends are close to the midline and point forward. The gland bends sharply laterally and anteriorly a short distance, then dips ventroposteriorly, turns toward the midline at the posterior margin of the 4th gastric segment, where the seminal vesicle joins it on its ventromedian surface. Beyond this junction each accessory gland tapers slightly, joins the gland from the other side, and forms a single tube. The first portion of this tube is the bound accessory gland duct, and the end portion where



the wedge is located is the ejaculatory duct. The bound accessory gland duct bends dorsally at the anterior edge of the 5th gastric segment.

The ejaculatory duct passes through the basal ring and between the anterior borders of the large, prominent, outer genitalic valves and enters the middorsal surface of the aedeagal bladder (Figs. 1 and 4). The posterior end of the ejaculatory duct is depressed into the middorsal wall of the aedeagal bladder.

The aedeagal bladder is a muscular-walled, ovoid sac that lies beneath the basal portions of the inner genitalic valves, and it opens posteriorly between the inner valves. Muscle fibers on the outer wall of the aedeagal bladder are attached to the anteroventral surfaces of the inner valves.

The accessory glands, the bound accessory gland ducts, the ejaculatory ducts and the aedeagal bladders in the *wilverthi* pupa and the *nigricans* adult and pupa are similar to those of the *wilverthi* adult.

Genitalia and Terminal Gastric Segments

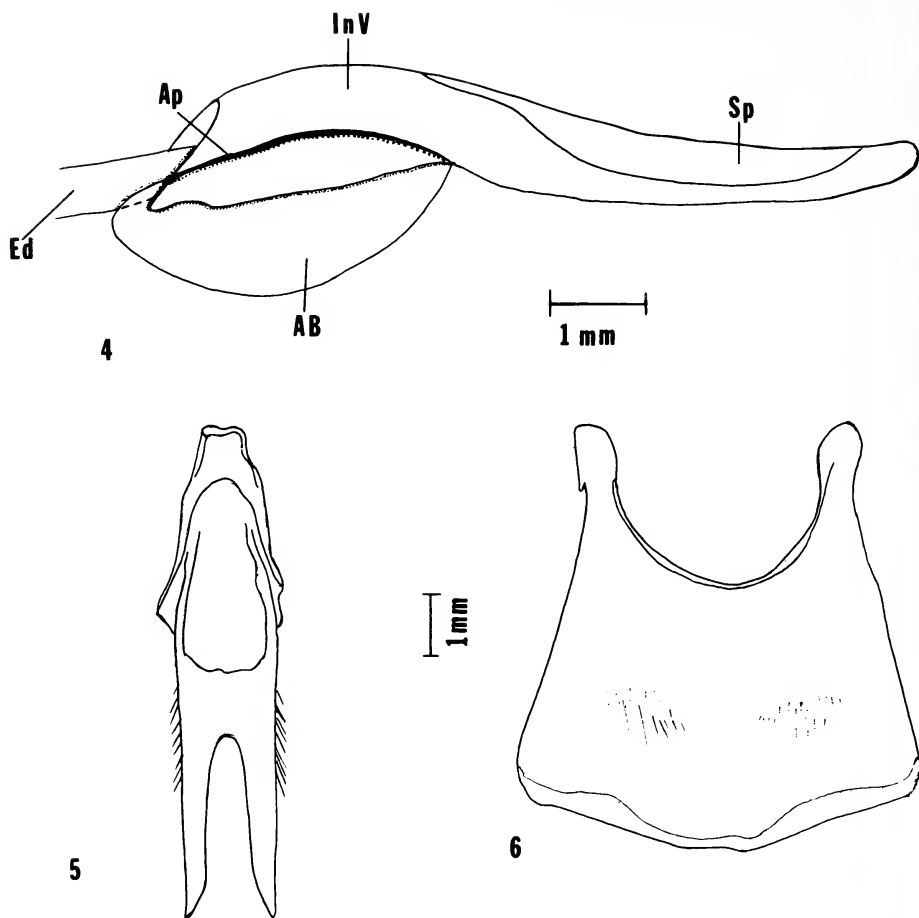
The external genitalia of *wilverthi* and *nigricans* (Figs. 1 through 6) are retracted into a cavity within the last few gastric segments beneath the rectum and the anus, and only the posterior tip of the ninth sternum or subgenital plate projects from the end of the gaster. This arrangement is characteristic of the dorylines (Borgmeier 1955). The external genitalia of these ants are composed of a basal ring and three pairs of valves, the outer, the middle, and the inner, typical of the formicid pattern (Clausen 1938; Snodgrass 1941; Krafchick 1959).

The basal ring or lamina annularis is a narrow, ring-like segment that is moderately sclerotized throughout (Figs. 2 and 3). The dorsal part is wider than the lateral and ventral portions, and it is fused to the dorsal, anterior borders of outer valves; its middorsal region forms a bridge between the outer valves. On the ventral part there is a small middorsal apodeme.

The outer valves or parameres are the largest and most heavily sclerotized of the three pairs (Figs. 2 and 3). They are laterally convex. From a side view the overall shape of the valve is somewhat C-shaped with the open part of the C directed downward. There is no division into an anterior lamina parameralis and a posterior paramere. The anterior portion of the valve is large and cup-shaped, and it covers the anterior tips of the middle valves and the bases of the inner valves. The posterior portion of the valve, when

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Figs. 2, 3. 2. Diagram of a lateral view of the male genitalia of *wilverthi*. 3. Diagram of a dorsal view of the male genitalia of *D. wilverthi*. Both diagrams are drawn to the same scale. Abbreviations: BR, basal ring; InV, inner valve; MV, middle valve; OV, outer valve; Sp, spermatheca.



Figs. 4-6. 4. Diagram of a right lateral view of the ejaculatory duct, the inner genitalic valve, and the aedeagal bladder of the adult male of *D. wilverthi*. Abbreviations: AB, aedeagal bladder; Ap, lateral apodeme; Ed, ejaculatory duct; InV, inner valve; Sp, spathe. 5. Diagram of the dorsal view of the ninth sternum or subgenital plate of the male of *D. wilverthi*. 6. Diagram of a ventral view of the eighth sternum of the male of *D. wilverthi*.

viewed laterally enlarges slightly. The ventral margin of this posterior portion is covered with numerous, long, slender hairs. Dorsally and ventrally the outer valves are separated from each other.

The middle valves or volsellares are the shortest of the three pairs, and they are finger-shaped (Figs. 1, 2, and 3). The basal portion is the tallest, and it tapers posteriorly. The ventroanterior part of the basal portion is joined to the ventroposterior tip of the base of the outer valve by bands of muscle. These middle valves lie within the posterior portions of the outer

valves, and they extend as far as or slightly beyond the posterior margins of the outer valves. The outer surface of these middle valves is convex. Fine, sensory hairs extend along the middle of the outer surface of this valve.

The inner valves or laminae aedeagales constitute the aedeagus or male intromittant organ (Figs. 1 through 4). The basal portion of the valve is laterally convex and has a ridge-like apodeme on its outer surface. Numerous bands of muscle extend from the lateral apodemes to the inner surface of the base of the outer valves. The remaining two-thirds of these valves are bent downward in the middle, they are scimitar-like in shape, and they are heavily sclerotized except at their tips. A heavy, non-sclerotized membrane, the spathe, joins these valves dorsally almost to their tips. A small triangular sclerite is present on its anterior end. These valves are also united ventrally by a membrane that extends almost to their tips. These valves extend slightly beyond the posterior margin of the outer valves.

The eighth sternum is roughly rectangular in shape and moderately sclerotized throughout (Fig. 6). Its anterior border is thickened and deeply indented, while the posterior margin is weakly sclerotized and rounded in shape. Two patches of dark, sensory hairs are present on its ventral surface.

The ninth sternum, or subgenital plate, is narrow in shape, bifid posteriorly (Figs. 1 and 5), and is heavily sclerotized throughout. The anterior margin is thick; in the central region of this segment there is a depression on the dorsal surface into which many muscle fibers are inserted. Here, also, there are two small, lateral, triangular apodemes. The ventral surface of the posterior end is covered with many sensory hairs. Posteriorly the tips of the segment extend beyond the end of the gaster and the posterior margins of the external genitalia.

In the *wilverthi* pupa the arrangement, shapes, and position of the valves and terminal gastric sterna are similar to those of the adult, but they are not as heavily sclerotized; in the adult they are dark brown in color. In the *nigricans* adult and pupa the arrangements, shapes, and positions of the valves and terminal gastric sterna are similar to those of *wilverthi*, and these structures in the pupa are less sclerotized. The genitalic valves and the terminal gastric sterna in *nigricans* are smaller in size, it is a smaller ant, and they are reddish-yellow in color.

Discussion

The testes in the adults and pupae of *wilverthi* and the pupae of *nigricans* are large and extend through the second and third gastric segments. The testes in the adults of *nigricans* are absent. In *N. harrisi* (Forbes and Do-Van Quy 1965) the testes are small and lie in the posterior region of the third gastric segment, in *E. hamatum* (Forbes 1958) they are large and

extend through the first three gastric segments, and in *D. labiatus* (Mukerjee 1926) no specific location was designated. The testicular follicles in both *wilverthi* adults and pupae, and *nigricans* pupae are long, slender tubules, 35–40 in each testis of *wilverthi* and approximately 50–55 in each testis of *nigricans*. The testicular follicles in *N. harrisi* and *E. hamatum* are long, slender tubules, 22–25 in each testis of *N. harrisi* and 20 in each testis of *E. hamatum*. In *D. labiatus* each testis contains “a fair number” of tubular follicles. The testicular follicles of all of the ants end in short narrow ducts, the vasa efferentia.

No connective tissue sheath covers the testes of the two *Dorylus* species herein reported. A single capsule covers the testes in *N. harrisi*, while each testis is covered by a capsule in *E. hamatum*. No capsule is reported by Mukerjee (1926) in *D. labiatus*. In *wilverthi* and *nigricans* the vasa efferentia join to form a short duct, the vas deferens. This arrangement is similar in *N. harrisi* and *E. hamatum*. Structures comparable to vasa efferentia are shown, but not labelled, by Mukerjee in his illustrations of the reproductive system of *D. labiatus*.

The seminal vesicles in *wilverthi* and *nigricans* adults and pupae are prominent, thick-walled, U-shaped tubes lying in the third and first half of the fourth gastric segments. In *N. harrisi* (Forbes and Do-Van Quy 1965) and *E. hamatum* (Forbes 1958) the position, shape, and arrangement of these organs are similar to that in *wilverthi* and *nigricans*. The terminology of this organ in male ants has been clarified by Hung and Vinson (1975). Mukerjee (1926) reports an organ in *D. labiatus* that he calls the seminal duct and describes a swelling at the anterior end, the collecting sac, and a larger dilation at its posterior end, the vesicula seminalis. He reports that this organ is usually U-shaped and also notes variations in the position and size of the vesicula seminalis. In this study nothing resembling the description and diagram of the seminal duct of *D. labiatus* was found.

The accessory glands in the adults and pupae of *wilverthi* and *nigricans* are prominent, thick-walled, S-shaped tubes lying in the fourth gastric segment. In *N. harrisi* and *E. hamatum* the accessory glands are tightly coiled tubes situated on either side of the intestine in the fourth gastric segment. The accessory glands of *D. labiatus* are large, slightly curved, thick-walled tubes, which in some cases have an appendix. Mukerjee indicates variations and anomalies in the reproductive system of *D. labiatus*. No such anomalies or variations were observed in the small number of specimens available for this investigation.

The bound accessory gland duct in *wilverthi* and *nigricans* is very short. In *N. harrisi* this organ is approximately equal to the accessory gland in length. In *E. hamatum* this duct encircles the ventriculus five or six times and is 28 to 31 mm in length. In *D. labiatus* no bound accessory gland duct

is reported, although a portion of what is shown as the ejaculatory duct may be the bound accessory gland duct.

The ejaculatory duct in *wilverthi* and *nigricans* is similar to that of *N. harrisi* and *D. hamatum*, and in all these ants a cuticular wedge is present in this organ. The ejaculatory duct, illustrated by Mukerjee (1926) in *D. labiatus* appears to be long, and he shows a wedge-shaped structure in the posterior part of this duct which he designates "penes." He found in a single specimen a blind diverticulum on the dorsal side of this duct. No such structure has been reported in any other doryline.

An aedeagal bladder is present in *wilverthi*, and *nigricans* as well as *N. harrisi* and *E. hamatum*. Mukerjee (1926) made no mention of this organ in *D. labiatus*.

The valves of the external genitalia and the terminal gastric sterna of these two *Dorylus* species show no individual variations, other than size, in their shapes. This is contrary to what Borgmeier (1955) reported in his study of the Neotropical dorylines where even in what may be related species distinctive differences are present in some genitalic valves and the subgenitalic plate.

Important differences, therefore, exist between the male reproductive systems of the two African *Dorylus* species herein studied and the two New World dorylines previously reported. The *Dorylus* species have a larger number of testicular follicles, the shapes of their accessory glands are different, the basal ring of the genitalia is fused to the outer valves, a membrane joins the ventral margins of the inner genitalic valves, and the shapes of the genitalic valves and the subgenitalic plate are different.

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Department of Biological Sciences, Fordham University, Bronx, New York 10458.

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APPARENT NEST SITE COMPETITION BETWEEN THE PAPER
WASP *POLISTES FUSCATUS* (HYMENOPTERA: VESPIDAE)
AND THE HOUSE WREN

David L. Gibo

Abstract.—Small colonies of *Polistes fuscatus* can suffer significant mortality due to attacks by house wrens. The wrens apparently compete with the wasps for nest sites.

The house wren *Troglodytes aedon* uses a variety of cavities as nest sites, including nest boxes, discarded tin cans, holes in banks, natural cavities in trees or stumps and bleached skulls of livestock (Bent 1948). Colonies of social wasps, particularly of the genus *Polistes*, also make use of similar nest sites and have been recorded in nest boxes (McAtee 1929, 1931), discarded tin cans and similar items (Rau 1942), holes in banks (Hungerford and Williams 1912) and cavities in trees and skulls of livestock (Rau 1931, 1942). Consequently, it is not surprising that there are occasional records of wrens and other small birds being displaced by social wasps (Bent 1948; Hart 1941; McAtee 1929, 1931). However, because the male house wren is exceedingly aggressive, he attempts to occupy all available nest sites in his territory (Bent 1948), *T. aedon* is potentially capable of competing with social wasps.

This note reports on a nesting pair of *T. aedon* that systematically exterminated approximately 15-17 colonies of the social wasp, *Polistes fuscatus* (Fabricius) during apparent competition for nest sites. The study area was located at the Wasp Studies facility on the Erindale Campus of the University of Toronto, Ontario, Canada. The particular location, which has been described previously (Gibo 1978), consists of two sets of nest boxes (sites A and B) and an abandoned shed located in a field adjacent to a woodlot. At site A 40 nest boxes were arranged in a 5×8 grid, with each nest box approximately 0.75 m from any other nest box. At site B 8 nest boxes were arranged in a 2×4 grid. The two sets of nest boxes were separated by approximately 20 m. The shed was approximately 20 m from nest box site A and 10 m from site B. The facilities had been utilized by a resident population of *P. fuscatus* for the past 6 seasons.

Poultry screen, with openings of 2.5 cm in diameter, was placed over the openings of the nest boxes and the windows of the shed. The screen was installed to protect the *P. fuscatus* colonies from attacks from birds, chiefly blue jays, red-winged blackbirds, Baltimore orioles, and other medium size species that are known to prey on *P. fuscatus* colonies in early summer (Gibo 1978). House wrens, which had not been observed at the facility in previous seasons, were able to slip through the poultry screen.

The pattern of colony initiation for *P. fuscatus* was typical. Foundresses initiated colonies in April or May and often were joined by other foundresses. By mid-June approximately 20–45 colonies were established in the study area and these remained active for the rest of the season. The colonies increased in size steadily and the first workers appeared by late June to early July. Although small nests with only a few cells were often abandoned early in the season, they were not knocked down and remained in place, empty and deserted, throughout the season. Predation on the colony by birds normally does not occur in this area until late June or early July, and in past seasons was prevented at the nest boxes with the screen (Gibo 1978).

In the spring of 1979 the normal pattern of colony development was observed at grid A until May 22 when a colony, with two foundresses and 13 cells, was found knocked down and all eggs and adults were missing. By this date at least 13 and possibly 15 colonies already were established. On June 5 three more colonies, one a two foundress colony with 12 cells, and the rest single foundress colonies, were found destroyed. All had constructed at least 10 cells and, judging from records of previous years, normally would have survived. Piles of twigs were found on the bottoms of two of the nest boxes that had been occupied by the *P. fuscatus* colonies. By June 12 all of the initial colonies were either destroyed or deserted and piles of twigs (nest building efforts of the *T. aedon* male) were found in all but two nest boxes. The pattern of colony development was similar at grid B. Two colonies were initiated and both were destroyed by early June. The nest boxes received deposits of twigs. A female joined the male on approximately the first of June and one of the nest boxes was subsequently utilized to rear a brood.

The colonies at the shed had a normal season. Nineteen colonies were established by mid-May, 18 of which were still surviving by mid-June. The single failure was not associated with destruction of the nest, but with loss (or desertion) of the single foundress. Colonies in the shed were completely destroyed by birds on two previous occasions, both in early July. The first attack occurred early in the study, prior to installation of the poultry screen on the shed windows. The second attack occurred two years later when birds entered through a hole near the door. This year the wrens apparently avoided the colonies in the shed.

The complete extermination of the box nesting colonies at the study sites differs from reports of other bird-*Polistes* interactions. It has been documented that birds prey on the adult wasps and brood, and usually attack prior to or shortly after the emergence date of the first few workers. At this time the colonies represent a large and relatively defenseless food supply (Gibo 1978; Gibo and Metcalf 1979). Although the house wrens may have been feeding on the wasps, the behavioral patterns observed, including (1) removal of all *Polistes* nests in boxes, regardless of size (most nests only contained a few eggs when removed), (2) filling the nest boxes with sticks,

and (3) ignoring the *P. fuscatus* colonies in the shed, indicate that competition for nest sites was the main *Polistes*-wren interaction. Consequently, territorial behavior and nest site competition by house wrens appears to represent a major threat to *P. fuscatus* colonies during the early period of colony initiation and may occasionally be responsible for local extinction of a concentration of colonies. Despite the tendency of the *P. fuscatus* foundresses to initiate colonies in the immediate area of the parental nest site (Gibo 1972; Rau 1940; West-Eberhard 1969), the total destruction of local concentrations of colonies as a result of predatory or territorial activities of birds, suggests that dispersal must play a major role in maintaining the population.

Acknowledgments

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Department of Zoology, Erindale College, University of Toronto, Mississauga, Ontario L5L 1C6, Canada.

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OVERWINTERING OF *POLISTES FUSCATUS* IN CANADA: USE OF
ABANDONED NESTS OF *DOLICHOVESPULA ARENARIA*

David L. Gibo

Abstract.—Over 350 females of the social wasp *P. fuscatus* were found overwintering in southern Ontario in two old *D. arenaria* nests. Most of the wasps were in a damaged nest that was attached to the southern side of a building and fully exposed to the sun. Mid-winter mortality was 2.8% or less. A test nest fitted with thermistors and placed in the original location of nest A showed that although the overwintering wasps can occasionally gain a moderate amount of protection (2.5°C) from low ambient temperatures in the intact nest, there was essentially no protection in a damaged nest. This study presents further evidence that adult *P. fuscatus* can survive nearly complete exposure to the midwinter temperature regime of southern Ontario.

Young queens of the social wasp genus *Polistes* are very opportunistic in their choice of overwintering sites and often appear to require only modest protection from the weather. Various species have been found overwintering in a variety of natural and man-made sites, including cracks and crevices in buildings (Gibo 1972; Snelling 1954; West-Eberhard 1969), under shingles and loose tarpaper (West-Eberhard 1969; Gibo unpublished data), in crevices in rocky bluffs (Rau 1930), under bark (Bohart 1942) and in stumps (Hermann et al. 1974). The wasps were often found in clusters, and several species may be present (Bohart 1942; Hermann et al. 1974; Snelling 1954). Old abandoned *Dolichovespula* nests are also utilized by *Polistes* as hibernation sites. Green et al. (1976) found 39 *P. fuscatus aurifer* queens in a nest in southeastern Washington and Zabriskie (1894) collected two *Dolichovespula* nests from buildings during winter in New York and found approximately 160 overwintering *Polistes* in each.

The occasional discovery of large numbers of *Polistes* in old *Dolichovespula* nests suggests that the wasps may select the nests, when available, in preference to other sites. However, the advantages in utilizing the abandoned nests are not readily apparent. Although these aerial nests are usually inaccessible to some potential predators active during winter, such as shrews and ground dwelling rodents, they are vulnerable to other predators such as squirrels, raccoons and birds. Furthermore, the old nests would be expected to offer little protection from low winter temperatures. The insulating properties of *Dolichovespula* nests are known to be relatively modest, and nest temperatures significantly higher than ambient temperatures are

only achieved through large energy expenditures by a population of active adult wasps (Gibo et al. 1974a, 1974b, 1976). An abandoned nest occupied by inactive *Polistes* should, with some lag, simply track the air temperature. The extent of the lag depends upon the effectiveness of the insulation, the rate of change in the air temperature, and the weather (particularly wind velocity). When air temperatures drop rapidly and then rebound the insulating properties of the nest material could, under favorable conditions (primarily little or no wind), have a moderating effect on the nest temperature. Of course, this moderating effect will also apply during brief periods of high ambient temperatures. A slightly more moderate temperature regime and a reduced amplitude in the daily temperature fluctuations, could, on occasion, be important for *P. fuscatus* survival. However, the actual thermal environment of old *Dolichovespula* nests during winter is unknown. The purpose of this note is to (1) report the use of old *Dolichovespula* nests by *P. fuscatus* in Canada, (2) report the midwinter survival rate of these wasps, and (3) examine the effectiveness of an old *Dolichovespula* nest in moderating the winter temperature regime.

Two old nests of *D. arenaria* were collected in midwinter in southern Ontario and examined for *P. fuscatus*. Nest A was collected on January 2, 1979. This nest had been partially destroyed by winter storms in 1978 and was missing part of its envelopes, partially exposing the combs on one side. It contained 354 *P. fuscatus*. Nest B was collected on January 11, 1979 and contained only 7 *P. fuscatus*. Midwinter mortality was low for both groups: 2.8% (10 wasps) for nest A and 0% for nest B. All of the overwintering *P. fuscatus* were females and, presumably, young queens. (West-Eberhard (1969) reported that all overwintering and overwintered *P. fuscatus* females that she examined (N = 28) during her studies in Michigan were found to be inseminated, and thus were potential queens.) In nest A a few wasps were found overwintering between envelope layers but most were either clustered on the combs or wedged head first into the cells. This latter posture is often observed when *P. fuscatus* are collected from their own nests in the fall. The wasps in nest B were clustered between the combs. Approximately 20 overwintering Diptera (Tachinidae) were also found in nest A.

The sites of the two old nests were similar. Both were attached to the overhang of the roof of a four-storey concrete building of the Erindale College campus of the University of Toronto. The nests were attached to the outer edge of the overhang, approximately 2 meters from the walls and 20 meters above the ground. Nest A was located on the southern side of the building and nest B was on the northern side. The difference in occupancy of the nests may have been due to the late season activity of the wasps. Every sunny day during the late summer and fall large numbers of *P. fuscatus* males and females were observed to gather on south facing walls of the building in the afternoon. The male wasps attempted to mate with pass-

ing females while the females spent much of their time investigating cracks and crevices in the masonry, apparently searching for overwintering sites. During the same period only an occasional wasp was observed on the shaded north facing walls.

In order to investigate the thermal environment of an old *D. arenaria* nest an intact nest that had been attached to a branch was obtained in the fall of 1979 and fitted with 2 thermistor probes. The probes were placed in the sections of the nest occupied by the overwintering *P. fuscatus* in nest A: between the central combs and in space between the roof of the nest and the top comb. Two additional probes were placed near the nest (5 cm and 1 m) to monitor air temperatures. The entire apparatus was clamped to a pole and, in early January of 1980, was securely attached to the overhang of the roof at the original location of nest A. Data were collected for 10 days. Records of the ambient temperature, nest temperatures and wind velocity were recorded in the early morning, midday, and late afternoon or whenever the ambient temperature was unusually high or low.

The results showed that an intact nest did provide some protection. During the first three days the ambient temperature ranged between -8° and $+1^{\circ}\text{C}$ and the nest temperature between -7.5° and $+3^{\circ}\text{C}$. When there was little wind (velocity < 2 km/hr) and the ambient temperature was changing rapidly, nest temperatures 2.5°C warmer than the ambient temperature were recorded. These differences occurred during the late afternoon and in the midmorning. When the nest was shaded and the ambient temperature was stable or changing slowly, and when wind velocities were approximately 5 km/hr or greater, nest temperatures were equivalent to the air temperature. However, on clear days exposure to the sun could warm the interior of the nest by approximately $+2^{\circ}$. The space between the top comb and the roof of the nest proved to be the most insulated area (i.e., experienced the least change).

After the third day of observations a winter storm removed part of the nest envelopes and partially exposed the combs on one side. The damaged test nest now was in approximately the same condition as nest A when it was occupied by overwintering *P. fuscatus* in January of 1979. As would be expected, the thermal regime of the test nest changed. During the next six days the weather was unsettled and measurements were made under a variety of combinations of wind, cloud cover, and temperature. The ambient temperature ranged between -9.5°C to $+2^{\circ}\text{C}$, and the nest temperature ranged from -9°C to $+7^{\circ}\text{C}$. In cloudy periods and at night the nest temperature was always within 0.5°C of the ambient temperature. During the midday when the nest was exposed to full sun it apparently trapped heat, and nest temperatures 5°C higher than the ambient were recorded, even on days when the wind velocity was approximately 15 km/hr.

The nest temperature records indicate that under certain weather conditions an intact *D. arenaria* nest can moderate the ambient temperatures by 2.5°C. This difference may occasionally be significant for *P. fuscatus* survival, particularly when the ambient temperature drops a few degrees below lethal levels for a relatively short period (e.g., before dawn). Although many overwintering *P. fuscatus* are very tolerant of low temperatures, and can survive at least 48 hours at -20°C, they are killed by exposure to 48 hours at -25°C (Gibo 1972, 1976). Temperatures approaching or falling within the lethal range usually occur in southern Ontario each year (Gibo 1972, 1976). Since nightly lows of -17°C had already been recorded at the College prior to the time the wasps in nests A and B were collected in January of 1979, the wasps in nest A had probably experienced these temperatures with little or no moderation.

A reduction of the amplitude of the daily temperature fluctuations only occurred within the intact nest and was restricted to overcast days with little or no wind. On sunny days the test nest had approximately the same or a greater daily temperature fluctuation than the ambient temperature. Exposure to the sun caused even greater fluctuations when the test nest was damaged. Because survival of *P. fuscatus* was high in a damaged nest exposed to the sun, the amplitude of these fluctuations does not appear very important to the wasps. This assertion is supported by other studies that show that overwintering *P. fuscatus* are capable of withstanding frequent cycles of freezing and thawing (Gibo et al. 1976).

In summary, a relatively modest moderation of the winter thermal regime can be obtained by *Polistes* that overwinter in old *D. arenaria* nests. This moderation occurs under specific conditions: an undamaged nest, little or no wind, no exposure to sun, and a rapidly changing ambient temperature. When any of these conditions are not met the nest temperature equals, or in some cases exceeds the ambient temperatures. Since the lowest temperatures usually occur at night, and often persist for several hours, little or no thermal moderation should be experienced by *P. fuscatus* overwintering in old *D. arenaria* nests during these critical periods. Possibly the abandoned nests offer their advantages to overwintering wasps. In addition to shelter from rain, snow and ice storms, the nests provide partial protection from the drying effects of the wind. The temperature data indicated that even damaged nests can provide this protection. Humidity is another consideration. When ambient temperatures are above 0°C, nests which have been recently soaked by rain would maintain high humidities. Whether this effect would persist at temperatures below 0°C remains to be determined. In any case, the study offers further evidence that overwintering *P. fuscatus* are sufficiently cold hardy to survive nearly complete exposure to the midwinter temperature regime of southern Ontario.

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Department of Zoology, Erindale College, University of Toronto, Mississauga, Ontario L5L 1C6, Canada

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POPULATION TRENDS OF THE ALFALFA WEEVIL
(COLEOPTERA: CURCULIONIDAE) AND ITS ASSOCIATED
PARASITES IN MARYLAND AND NEW JERSEY, 1966-1970

Robert F. W. Schroder and William W. Metterhouse

Abstract.—Populations of the alfalfa weevil, *Hypera postica* (Gyllenhal), in Maryland and New Jersey and of associated parasites changed greatly in the period 1966-70. The alfalfa weevil declined rapidly during the period under the increasing pressures of the introduced parasites *Bathyplectes curculionis* (Thomson), *Tetrastichus incertus* (Ratzeburg), *Microctonus colesi* Drea, *Microctonus aethiopoides* Loan and *Bathyplectes anurus* (Thomson).

The biology and ecology of the alfalfa weevil, *Hypera postica* (Gyllenhal), and of the associated parasites in Maryland and New Jersey were reported for the period 1961 to 1967 by Blickenstaff et al. (1972). This study included details concerning the life history, habits, and movement of the weevil, the importance of fall-laid eggs, the number of generations/year, the levels of populations, the establishment, spread and percent parasitism of introduced parasites, and the results of surveys of fall and winter populations of adults done so investigators could predict larval populations and damage. Much other work done on the biology and life history of the alfalfa weevil was listed by Cothran (1966).

The population surveys of the alfalfa weevil begun by Blickenstaff and Huggans (Blickenstaff et al. 1972) in 10 fields in Maryland and New Jersey in 1964 and 1965 were continued and are reported here for the period from fall 1966 to spring 1970. The fields in Maryland and New Jersey that were surveyed from fall 1966 through March 1968 were the same as fields surveyed by Blickenstaff et al. (1972). Thus, Maryland fields 1 and 2 were in Howard County, near Clarksville; fields 3, 4, 5, and 6 were at Beltsville, Prince George's County; field 7 was in Howard County near Jessup; fields 8 and 9 were at Crownsville, Anne Arundel County; and field 10 was in Montgomery County near Rockville. In New Jersey, the survey fields established by Blickenstaff in cooperation with the New Jersey Department of Agriculture were: fields 1 and 2 in Sussex and Warren Counties in the upper Appalachian Valley; field 3 in Warren County in the Lower Appalachian Highlands; fields 4 and 5 in Hunterdon and Mercer Counties in the Lower Appalachian Piedmont area; and fields 6-10 in Monmouth, Burlington, Gloucester, and Cumberland Counties in the Inner Coastal Plain area. The single major change in field locations was made in March 1968 when 8 out of the 10 Maryland fields were dropped and 8 new fields were chosen.

This change was made to provide a more complete evaluation of weevil populations in the major alfalfa producing areas of central and western Maryland. Two of the original 10 fields (field 9 at Clarksville and field 10 at Beltsville) were retained for comparison. The new locations were: fields 1 and 2 at Goshen and Boyds, Montgomery County; fields 3 and 6 at Frederick and Thurmont, Frederick County; fields 4 and 5 at Boonesboro and Smithsburg, Washington County; and fields 7 and 8 at Westminster and Sykesville, Carroll County.

To maintain uniformity in sampling and analysis of the data collected, we determined populations of larvae from April through July by examining plant material (foliage) from 1- or $\frac{1}{2}$ -ft² samples or removed adults from ground samples during the winter season with a suction device. However, in March 1968 the number of samples ($\frac{1}{2}$ ft²) for adult alfalfa weevil collections was increased from 10 to 20 per field. The sampling of insects in the field and the processing of samples in the laboratory were generally the same as those reported by Blickenstaff et al. (1972), and where modifications were introduced, they are noted.

Until 1968, adult alfalfa weevils were collected October through March from each field with a D-Vac suction machine designed and developed by Dietrick (1961). However, when more extensive field surveys were undertaken in 1968, the machine was mounted on wheels to reduce the time, labor and fatigue involved in sampling (Schroder 1970). The adults that were collected with the vacuum were separated from debris by sieving and then collected by forceps and counted.

Collections of larvae were made by cutting ten $\frac{1}{2}$ -ft² foliage samples at ground level and placing the foliage with the insects in paper bags. The samples from the 10 New Jersey alfalfa fields were collected by personnel of the New Jersey Department of Agriculture and then processed at Beltsville, Maryland. The samples from the 10 Maryland alfalfa fields were collected by personnel of USDA and processed at Beltsville. A maximum of 50 3rd–4th instar larvae were removed from each of the foliage samples and placed with a fresh bouquet of alfalfa in a container. The container consisted of a 6 in. glass tube (2" diam.) sealed at one end with parachute cloth and a cork with a vial inserted in the center at the other end. The alfalfa was placed in the vial and sealed with a sponge. This provided a cage for the larvae to develop to adults. The cages were checked daily for the emergence of parasites from the larvae. Additional collections of larvae were made by sweeping the alfalfa at times when low numbers of larvae were present. Foliage samples were then processed by using a high-speed blender-water extraction technique (Schroder 1974) instead of the alcohol-kerosene method of Blickenstaff and Huggans (1969). By the new procedure, the 1st to 4th instar larvae were dislodged from the alfalfa in a high speed blender and then separated from the debris by washing through a series of sieves. The

number of larvae/ $\frac{1}{2}$ ft² was then determined by totaling the number obtained for recovery of parasites and the number recovered by extraction. Then the number of larvae/ft² for each field could be calculated and recorded.

Microctonus colesi Drea (Braconidae) and *M. aethiopoides* Loan (Braconidae), parasites of adult alfalfa weevils, are difficult to recover because of the diapause of the host and the diapause of the parasite larvae in the host. Neal et al. (1971) demonstrated that topical application of the juvenile hormone cis-trans and trans-trans 10,11 epoxyfarnesenic acid methyl ester brought forth larvae of both *Microctonus* parasites. Once the parasite larvae emerge from the host and if adult *Microctonus* did not emerge, species identification was a problem. There were no dependable external body characters available for use in distinguishing the larvae of these parasites until Fuester (1970) separated them by the size of their mandibles.

There were three methods used to determine parasitism of adults: 1) hold the weevil adults on fresh bouquets of alfalfa in small cages until the parasites emerge, 2) dissect adults, and 3) treat with synthetic juvenile hormone. Depending on the availability of the hormone, it was applied topically on the venter of the abdomen with 100 μ g of the hormone in 0.5 μ liter acetone with a microinjector. The weevils were then held for emergence of parasites for 30 days and then dissected to determine presence of parasite larvae.

Alfalfa Weevil Adult Populations

1966–1967

Surveys for alfalfa weevil adults begun in September 1966 in Beltsville, Maryland signaled that the adults did not start to return to alfalfa fields until early October and reached a peak, a high of 6.7 adults/ft², in mid-November (Table 1). Numbers then declined by 67% to 2.3/ft² in mid-March 1967. A similar decline was apparent in New Jersey fields, although only 2 collections were made. The fewer collections made in New Jersey make it difficult to pinpoint the peak population for this area as accurately as for Maryland, but we feel that the figures in Table 1 provide a valid estimate of the levels. Thus, populations in New Jersey were approximately $\frac{1}{2}$ those in Maryland, but the declines (63%) from mid-November to mid-March were very similar. The same approximate 2 to 1 difference in adult numbers in Maryland vs. New Jersey and the $\frac{2}{3}$ decline in adults was reported by Blickenstaff et al. (1972) for the winters of 1964–66.

1967–1968

Regular collections were put off until October 30, 1967, in Maryland because earlier collections in Beltsville were not successful. The totals showed fewer alfalfa weevils than in 1966 and a later return of the adults to the fields

Table 1. Alfalfa weevil adults/ft² in 10 Maryland and 10 New Jersey survey fields. 1966–1970¹.

Date	1966–1967	
	Maryland	New Jersey
9/23	.02	—
10/20	2.86	—
11/14	6.66	—
11/17	—	3.54
12/12	4.74	—
1/17	2.92	—
2/27	1.30	—
3/16	2.26	—
4/4	—	1.32
1967–1968 ²		
10/30	1.24	—
11/21	—	1.36
11/20	1.68	—
12/19	2.26	—
3/25	1.63	—
3/27	—	.88
1968–1969		
11/22	.51	—
12/20	.29	—
1/16	—	.18
1/27	.16	—
2/19	.15	—
3/11	.14	—
4/8	—	.26
4/11	.76	—
4/19	.45	—
4/24	.41	—
1969–1970		
10/14	.43	—
10/22	.51	—
10/30	.51	—
11/24	.96	—
12/3	.48	—
12/11	.77	—
2/27/70	.11	—
3/10	.23	—
3/26	.21	1.4
4/29	.66	—

¹ Average for 10 fields, 10 ½ ft² samples/fields. — = no samples taken that date.² Sample size for adult collections was increased from 10 to 20 ½ ft² samples/field. Change effective from 3/25/68–4/29/70.

(Table 1). Populations peaked at 2.3/ft² in mid-December and declined to 1.6/ft² by late March, a reduction of only 30%. In New Jersey, populations were again about ½ those in Maryland and the overwinter reduction was 35%. This was the first year since the surveys were begun in 1964 that the decline in numbers of adults from fall to spring was less than 60%. This sharp reduction in measurable overwintering mortality plus the late return of adults in the fall of 1967 suggests that fewer adults returned to the fields in the fall, but that larger numbers than normal returned in the spring. Such spring migrations of adults had not previously been considered important in the Maryland–New Jersey area, but are a common occurrence in New York (Poinar and Gyrisco 1962).

1968–1969

Collections of adults in both states in the fall of 1968 showed greatly reduced populations and much later appearance of adults, confirmation of the trend reported for 1967 (Table 1). As in 1967, this late return was signaled by failure to collect them in numerous alfalfa fields in the Beltsville area. For this reason, regular collections were not begun until November. Although populations were low throughout the 1968–69 season, numbers of adults were actually higher in the spring of 1969 than the previous fall, another indication of change in the migration of the weevil. The trend was obvious in both states though populations remained lower in New Jersey than in Maryland.

1969–1970

D-Vac sampling was begun October 14, 1969, when the first adults were recovered by sweeping. Once again, populations in Maryland were relatively low (Table 1), and the decline in overwintering Maryland adults was lower than in the 1966–67 season. In New Jersey, sampling was not done during the fall season; however, the samples taken in March 1970 showed an average 1.4 adults/ft², an increase over the average for the spring of 1968 and 1969.

Alfalfa Weevil Larval Populations

The mean numbers of alfalfa weevil larvae/ft² for the 10 Maryland and 10 New Jersey alfalfa fields (calculated from the combined means of the larvae/ft² in individual fields) are shown in Figures 1 and 2. In 1967, larval populations peaked earlier than anticipated in both states and reached the highest levels seen since the surveys were begun in 1964, 370 and 265 for Maryland and New Jersey, respectively (Figs. 1 and 2). Populations in both states remained above the 100 larvae/ft² level for over 6 weeks. The New Jersey peak occurred approximately 3 weeks later than the Maryland peak.

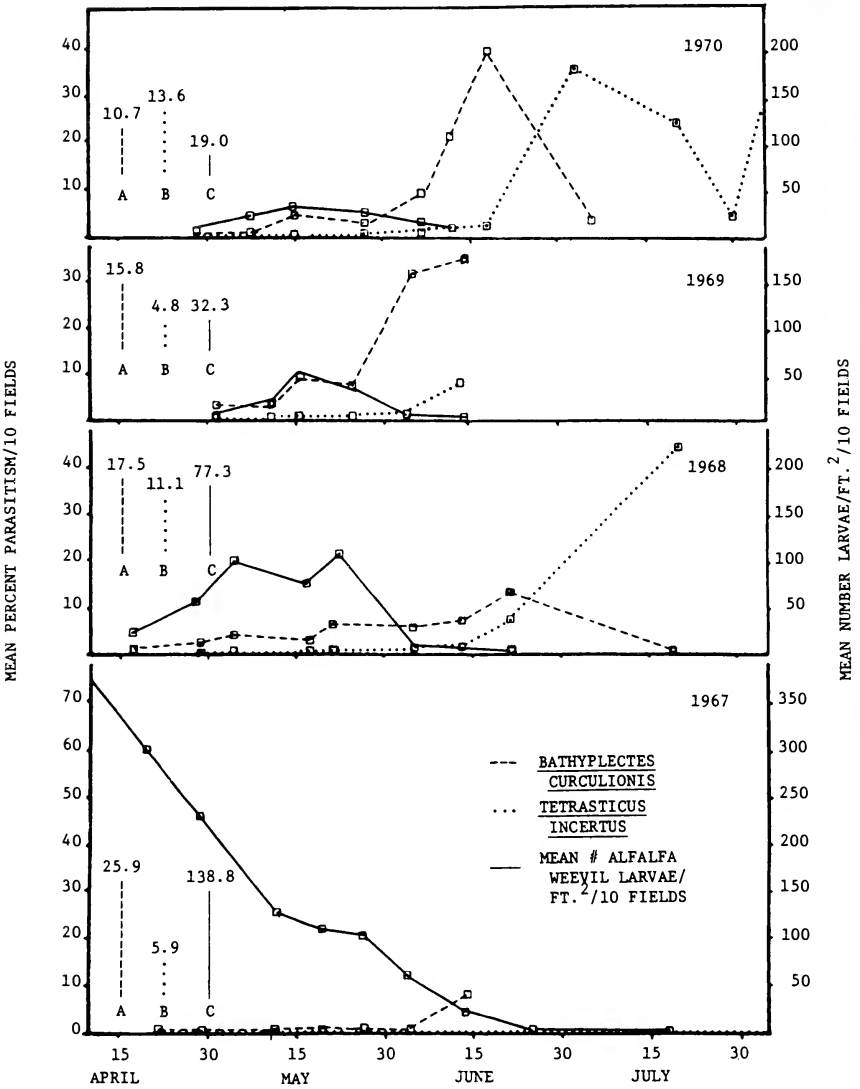


Fig. 1. Maryland: Mean number alfalfa weevil larvae/ft² per 10 fields (—) and mean percent parasitism of the larvae by *B. curculionis* (- - -) and *T. incertus* (. . .), 1967–70. The figures A B C represent the pooled standard deviations of the means.

In 1968 the larval buildup peaked almost one month later than in previous years in Maryland and 2 weeks later in New Jersey. In addition, the average number (over 10 fields) for both states was 75% of that for 1967 (100% in Maryland and 65% in New Jersey). In Maryland, populations remained at

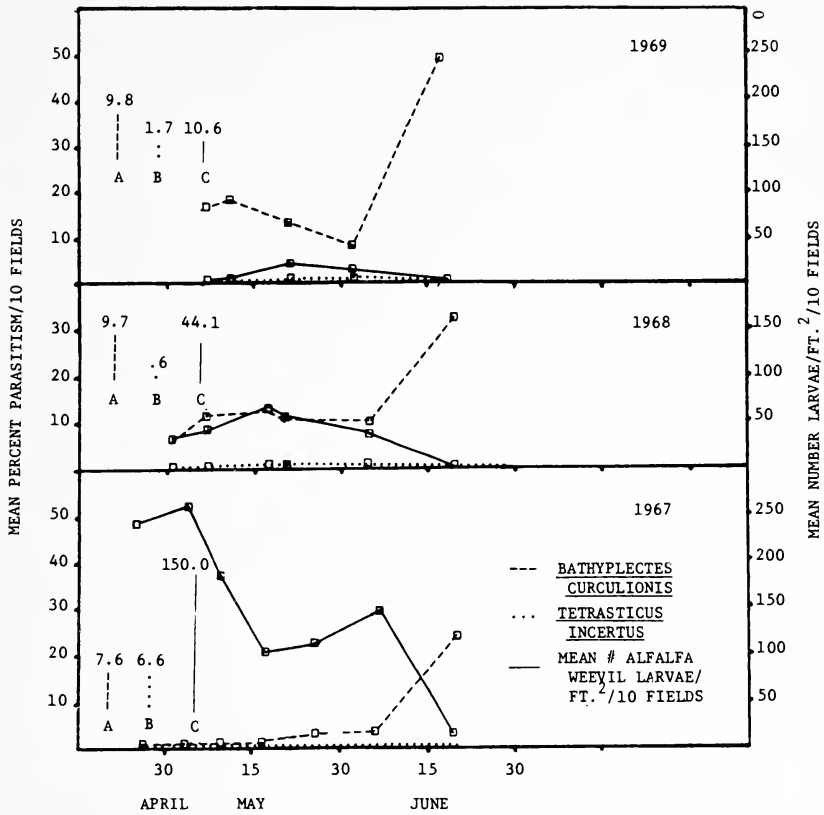


Fig. 2. New Jersey: Mean number alfalfa weevil larvae/ft² per 10 fields (—) and mean percent parasitism of the larvae by *B. curculionis* (- - -) and *T. incertus* (. . .), 1967–69. The figures A B C represent the pooled standard deviations of the means.

the peak level for about 2 weeks, which created a plateau rather than a sharp peak as in previous years (Figs. 1 and 2).

Alfalfa weevil larval populations in 1969 were lower in both states than in 1968. The peak in Maryland occurred about 1 week later than in 1968; the peak in New Jersey occurred about 1 week later than in Maryland. A comparison of the mean peak larval populations of the 10 fields in both states from 1967 to 1970 showed a 86 and 92% reduction in numbers of larvae/ft² in Maryland and New Jersey, respectively (Table 2).

In 1970 the larval populations declined to the lowest level since the surveys were begun (Figs. 1 and 2).

Thus, since 1967, the number of larvae collected in field 10 in Maryland, one of the two fields sampled all 4 years, has declined from a peak of 980

Table 2. Peak number of alfalfa weevil larvae for each of the 10 fields in Maryland and New Jersey, 1967-1970.

Field no.	Peak number larvae/ft ²							
	New Jersey				Maryland			
	1967	1968	1969	1970	1967	1968 ¹	1969	1970
1	157	62	21	45	316	41	77	27
2	168	76	18	10	531	231	46	71
3	133	27	35	35	557	45	39	12
4	401	93	21	18	585	129	140	38
5	351	45	30	9	544	334	161	58
6	194	55	15	17	147	97	61	28
7	124	103	12	7	541	65	14	63
8	532	211	32	16	169	96	49	31
9	813	216	7	17	320	84	42	26
10	593	67	81	20	980	86	49	29
x	346.6	95.5	27.2	19.4	469.0	120.8	67.8	38.3

¹ Fields 2 and 10 in Maryland sampled again in 1969; all others in 1969 were new locations.

to 29 larvae/ft². The overall decline was 92% for all 10 fields (Table 2). Nevertheless, there were some areas that had severe larval damage. In New Jersey, larval populations also declined by 92% and so have remained at about ½ the Maryland levels.

Correlations Between Adult and Larval Populations

Blickenstaff et al. (1972) indicated that correlation of adult alfalfa weevil populations collected in November and March with the peaks of larval populations that followed were helpful in predicting potential damage to alfalfa. It was one of the objectives of continuing the two-state surveys to predict potential damage from such correlations. The relationship between these adult numbers and the peak larval populations in individual fields is shown in Table 3. Significant correlations were obtained for Maryland fields in 1966-67 except for adults collected in February. Also, significant correlations were obtained for New Jersey fields for November 1966 and March 1968. Likewise, in 1968-69, significant correlations were obtained between Maryland adults collected in January and March and peak spring larval numbers and between New Jersey adults collected during April 1969 and the peak in spring larvae. Correlations were not obtained between Maryland adults collected in 1969 or 1970, and the 1970 peak larval populations and correlations were not available for the 1969-70 season in New Jersey because samples were not collected. The change in behavior of the overwintering adults in Maryland identified from the sampling is evident in the lack of the uniform correlation between adults and peak larval populations dem-

Table 3. Correlations between winter collected adult alfalfa weevil populations and peak larval populations the following spring.

Adults collected	1966-67		1967-68		1968-69		1969-70
	Md.	N.J.	Md.	N.J.	Md.	N.J.	Md.
Oct.							.19
Nov.	.85**1	.73*	.35	.05	.57		.21
Dec.	.73*		.18				.14
Jan.	.66*				.72*		
Feb.	.59						.32
March	.76**	.52	.37	.67*	.98**		.31
April					.51	.88**	.20

¹ ** Indicates significance at 1%. * Indicates significance at 5%.

onstrated by Blickenstaff et al. (1972). However, the significance of the correlations (Table 3), despite this change, support the idea that the number of overwintering adults can be helpful in predicting potential larval populations.

Parasites of the Alfalfa Weevil

The history of releases and recoveries of the alfalfa weevil parasites in Maryland and New Jersey was reviewed by Blickenstaff et al. (1972) and Dysart and Day (1976). It was the main objective of the continuing surveys to determine the incidence of and percent parasitism by alfalfa weevil parasites in the 10 alfalfa fields of Maryland and New Jersey.

Larval Parasites

As indicated, the alfalfa foliage in 1/2 ft² at 10 or 20 sites in each field on each sampling date was shaken to dislodge larvae and those in the 3rd and 4th stadia were held for parasite recovery. The supplemental surveys were processed in the same manner so we would have additional larvae, if necessary, to observe for parasite recovery. A maximum of 50 such larvae from each sample were placed in containers with fresh alfalfa and reared to adults in the laboratory at room temperature. The containers were examined weekly for emerging parasites.

Bathyplectes curculionis (Thomson) (Ichneumonidae), an introduced larval parasite, was the predominant parasite of the alfalfa weevil collected in the 10 Maryland and 10 New Jersey alfalfa fields from 1967 to 1970. In Maryland, the highest level of parasitism for a single field was 64% on June 20, 1968, in New Jersey, the highest level recorded was 61% on June 19, 1968. The increased synchronization between populations of *B. curculionis* and the peak population of alfalfa weevil larvae in Maryland and New Jersey

through the 1969 season that is shown on Figures 1 and 2 suggests an increased effectiveness of the parasite, especially in New Jersey. The mean percent parasitism of alfalfa weevil larvae by *B. curculionis* shown in these figures was calculated by using the means for percentage parasitism for the individual fields.

Bathyplectes anurus (Thomson) is another introduced larval parasite. It was recovered in 1970, for the first time in these surveys, in New Jersey. There it was parasitizing 30% of the larvae collected in field 7. The parasite was not recovered from larvae collected in any of the 10 Maryland alfalfa fields during the time of these surveys. This is not surprising since the first record for recovery of *B. anurus* in Maryland was in Prince George's County in 1972. The first record for recovery in New Jersey was in Monmouth County in 1967 (Dysart and Day 1976).

Tetrastichus incertus (Ratzeburg) (Eulophidae) is an introduced larval parasite that becomes abundant in Maryland and New Jersey alfalfa in late summer, generally after the first cutting when host density is low; it therefore appears later than the *Bathyplectes* species. This parasite has been established in Maryland since 1964; its spread and distribution in the eastern United States, especially in Maryland and New Jersey, was reported by Schroder et al. (1969). The incidence and mean percent parasitism of the alfalfa weevil by *T. incertus* in the 10 Maryland and 10 New Jersey alfalfa fields for the period 1967–70 was calculated by using the means for percentage parasitism for the individual fields and is shown in Figures 1 and 2. Plainly *T. incertus* parasitism increased very rapidly in the Maryland survey fields: it was 14% in 1967 and 73% a year later. Thus, it seems to be an effective late season parasite of alfalfa weevil larvae in Maryland. However, it was not recovered until September in New Jersey in 1967 and then only in the southern 4 fields; in 1968 and 1969, it was found in only 2–3 fields, and parasitism was less than 9%; and in 1970, it was recovered from only 2 fields, and there levels of parasitism were less than 2%.

Adult Parasites

According to Brunson and Coles (1968) the adult parasite *Microctonus aethiopoides* was firmly established by 1968 in about 100 square miles of area in central New Jersey. It was introduced into Maryland in 1965 at Beltsville but was not recovered through 1967 (Blickenstaff et al. 1972). The first record for recovery of *M. aethiopoides* in Maryland was in Frederick County in 1969 (Dysart and Day 1976). *Microctonus colesi*, another parasite of adult alfalfa weevils, was recovered in low numbers from both Maryland and New Jersey by the time of the reported surveys (Drea 1968).

In 1967, *M. colesi* adults were recovered from adult weevils collected in 5 of 10 Maryland fields where *Microctonus* parasitism ranged from 2 to

50%. In New Jersey, in 1967, *Microctonus* spp. parasites were collected from 4 fields, *M. colesi* from 2 (1 of the 6 adults and 1 of the 16 adults collected, respectively), and *M. aethiopoides* from 2 (1 of the 6 adults and 1 of the 8 adults collected, respectively). Also, collections of larvae made in spring of 1968 and held for adult eclosion showed *M. colesi* present in 3 of 10 New Jersey fields with 16.7% parasitized in field 10, 33.3% in field 7, and 66.7% in field 6. One *Microctonus* sp. emerged from 10 adults collected in field 3. In Maryland, collection of adults in the spring of 1968 showed *Microctonus* parasitism in 9 of 10 fields, always at rates less than 5.95%. However, when overwintering adult alfalfa weevils collected in Maryland fields during the winter of 1968–69 were dissected to determine percent parasitism by *Microctonus* spp., 5 of 10 fields contained parasitized adults, and parasitism ranged from 18 to 66%. Also, 1, 3 and 3 *Microctonus* immature parasites were recovered from adult weevils collected January 1969 from New Jersey fields 2, 8 and 9, respectively. In addition, *M. colesi* emerged from adult weevils collected April 1969 in 3 fields. Parasitism ranged from 20 to 33%.

In 1969, in Maryland, larvae were collected from fields in the spring and reared to adults. Then 50 of these adults from each collection taken in fields 3–8, and 10 were treated with the synthetic juvenile hormone to recover *M. colesi*. All living adults were then dissected 30 days after treatment to determine whether any more parasites were present in the host. *M. colesi* emerged from alfalfa weevil adults collected from 6 of the 7 fields and parasitism ranged from 2 to 22% (including the 3 recovered by dissection); the mean was 9.4%.

Microctonus aethiopoides emerged from adults collected in 1969 from Maryland fields 6, 8 and 9. No parasites emerged from adults collected in fields 1–5, and 10. The highest level of parasitism was 19.2% in field 6. In 1970, collections made in the 10 Maryland survey fields in spring showed *M. colesi* present in 8 fields and parasitism ranged from 12.5% in field 3 to 89.3% in field 4. Parasites were not recovered from alfalfa weevil adults collected in fields 7 and 10.

In New Jersey, alfalfa weevil adults were reared from larvae collected in spring 1969. These weevils were held for recovery of parasites until August 19, 1969. On this date 50 adults from fields 3–8, and 10 were each treated with 100 μ g of the same synthetic hormone used previously. As a result, *M. colesi* emerged from 2 to 16% of the adults collected from the 7 fields.

Summary and Conclusions

1. Adult alfalfa weevil population levels in New Jersey and Maryland declined steadily from 1967 until spring 1969, but collections from Maryland fields in fall 1969 showed a slight increase over the previous year. This

increase was not reflected by an increase of larvae the following spring. Adult population levels in New Jersey remained about $\frac{1}{3}$ to $\frac{1}{2}$ lower than population levels in Maryland.

2. Populations of alfalfa weevil larvae declined from a peak of nearly 1,000/ft² in 1967 to the lowest level recorded, less than 100/ft², in 1970. Despite this near 10-fold decline, there were isolated areas reporting serious damage. Larval populations in New Jersey for the 4 year period remained about $\frac{1}{2}$ to $\frac{1}{3}$ lower than larval populations in Maryland.
3. Previous to 1968, Maryland and New Jersey alfalfa fields had shown a characteristic decline in adult weevils from fall to spring of approximately 66%; however, the decline was not evident from 1968 to 1970. This change in behavior of the adult weevil was reflected in the lack of correlation between overwintering adults and peak larval populations for the three seasons, 1968–70. Nevertheless, correlations were obtained between spring adult populations and the subsequent peak larval populations for the period 1966–69, except for the March 1967 collections in Maryland. The conclusion of Blickenstaff et al. (1972) that the number of adults per given time is helpful in predicting potential larval populations is therefore supported.
4. *Bathyplectes curculionis* was the predominant parasite of the alfalfa weevils collected in all 10 Maryland and New Jersey alfalfa fields in 1967–70. The increased synchronization of peak populations of *B. curculionis* and the peak population of larvae in Maryland and New Jersey suggests an increased effectiveness of the parasite during that period, especially in New Jersey. The high levels of parasitism, from 64% in Maryland to 61% in New Jersey, and this increased synchronization made this a very effective parasite.
5. *Bathyplectes anurus* was recovered in 1970, the first recovery in these surveys, from one of the 10 alfalfa fields in New Jersey.
6. Parasitization by *T. incertus* built up very rapidly in Maryland fields from a low of 14% parasitism in 1967 to a high of 73% a year later. The parasite appears late in the season, generally after the first cutting and at a time of low host density. *T. incertus* give indications of being an effective late season parasite of alfalfa weevil larvae in Maryland. However, in New Jersey, *T. incertus* practically disappeared in 1968–70. The low parasitism levels may be a result of the much lower host density in New Jersey alfalfa fields.
7. *Microctonus colesi* and *M. aethiopoides*, parasites of adult alfalfa weevils, were difficult to recover because of the diapause of the host and the diapause of the parasite larvae in the host. Topical application of synthetic juvenile hormone to adult weevils induced early emergence of *Microctonus* parasites. Species identification was a problem if adult *Microctonus* did not emerge. However, based on the available data, both species are

established and increasing in the survey areas of Maryland and New Jersey.

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Beneficial Insect Introduction Laboratory, Agricultural Research, Sci. & Educ. Admin., USDA, Beltsville, Maryland 20705 and Division of Plant Industry, New Jersey Department of Agriculture, Trenton, New Jersey 08025.

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BOOK REVIEW

Herbivores: Their Interaction with Secondary Plant Metabolites. Edited by Gerald A. Rosenthal and Daniel H. Janzen. 1979. Academic Press, New York. 718 pp. \$59.50.

"Chemical ecology" is a maddening field. Almost devoid of theory (and utterly dependent on the coarse verbal "ploy-counterploy" model, which has changed little since proposed by G. Fraenkel in his classic paper "The raison d'être of secondary plant substances" 21 years ago), it consists largely of a collection of more or less pretty anecdotes. Yet the prettiest anecdotes are always the new ones; whenever a story is developed in detail, carried beyond the stage of descriptive natural history, its prettiness goes away and the evolutionary and functional scenarios become clouded. A good example is the phytoecdysones. There is indisputable appeal in the idea of plants outfoxing insects by confounding their development with large doses of hormone analogues. Yet most phytoecdysones that are ingested by insects are degraded by the midgut epithelium and cannot "function" in this way. In the "insect hormones" chapter of this new collection, Karel Sláma, who started this story going, sidesteps the degradation issue on page 693. Reese tackles it head-on on pp. 323-324.

"Herbivores"—the title is misleading and may help sales for the wrong reasons—is the latest attempt to integrate "chemical ecology." It brings together a great many pieces of the puzzle, but puzzle it remains. The field clearly still suffers from confusion over the concept of "function" in an evolutionary-biological context. The ecological and evolutionary chapters still suffer lapses into the unwarranted assumption that "compound X evolved in order to deter (poison) species Y" just because it is seen to do so now. This is tantamount to saying the function of DBCP is to sterilize workers in chemical plants!

Yet, full of hot air as they are—perhaps because they are—the ecological and evolutionary chapters are where the fun is. For most biologists the superb reviews of the major classes of secondary compounds are "chicken-wire chemistry" potentially useful for reference. Janzen's chapter, "New horizons in the biology of plant defenses," is outrageous as usual—and much to the point. "Herbivores do not eat Latin binomials," he says, reminding that Gertrude Stein did not mean a rose is a rose is a rose *biochemically*. Then he says "plants are anachronisms," and tells about things superbly adapted for seed dispersal by creatures which are extinct. (Phylogenetic inertia, the last refuge of scoundrels, is indeed untestable—and probably true.) His last two subheadings are "pitfalls" and "one-liners." Perhaps his next overview will include "pratfalls" and "howlers," both of which certainly apply in this field.

Among the various chapters, Chew and Rodman's stands out as a courageous (and ultimately unsuccessful, but that isn't important) attempt to calculate the energetic costs to a plant of defending itself chemically. The costs of defense have generated a lot of hot air, and this is the first attempt to do something concrete with the idea. Chew and Rodman don't succeed because it just isn't possible now to isolate that segment of the system from the plant as a whole, just the same as "optimization theory" in ecology has relied on extremely naive calculations which compartmentalize the time and energy budgets of organisms in questionable ways. A great many evolutionists act as if evolution can do *anything*. But the process of adaptation is non-Markovian; it does matter where you have been; and the mere fact that doing something is energy-inefficient means nothing about the opportunity of stopping. Perhaps lots of things are anachronisms, *sensu* Janzen.

Past work in this field has had a strong taxonomic bias; many "chemical ecologists" acted as if all herbivores had six legs. This book has less of an insect slant, but it still belongs on the shelf next to Keeler, VanKampen, and James' "Effects of Poisonous Plants on Livestock" (Academic Press, 1978) for the sake of balance. There are signs that phytopathologists, entomologists, vertebrate biologists, and vegetation scientists are finally converging on a common realization that the same compounds may have *multiple* "raisons d'être." This is all to the good. Anyone who considers him- or herself a "chemical ecologist" or "coevolutionary biologist" should have and read "Herbivores"; Janzen's cautionary chapter should be required reading for anyone considering doing this for a living. The cost of the book is ridiculous on its face, but decomposes to 8.3¢/page, which nowadays ain't all that bad.

The chemistry in the book is safe. Take the biology with a grain of salt (which, of course, may be dangerous to your health).

Arthur M. Shapiro, *Department of Zoology, University of California, Davis.*

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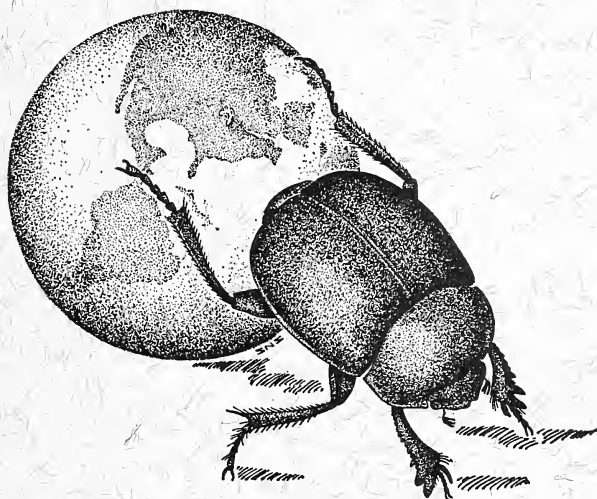
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ZOOLOGICAL

SU ZAN NOGUCHI SWAIN
(Mrs. William Kenneth Firmage)

Su Zan Noguchi, third of the five gifted daughters of Minosuke and Tomi Ogawa Noguchi, was born in Colorado. She attended the University of Colorado at Boulder, being graduated in 1938 with the degree of Bachelor of Fine Arts. Even before her graduation she had illustrated various biological publications for members of the university faculty.

While serving as Staff Artist for the School Nature League at the American Museum of Natural History she was married to Dr. Ralph B. Swain, a well known entomologist in the United States Department of Agriculture, by whom she later had two sons, Tom Alfred and Ralph Adrien. With Dr. Swain she prepared and illustrated *The Insect Guide* (Doubleday 1948), one of the finest and most successful of such popular works. Together, also, they wrote and illustrated the section on insects in *Compton's Pictured Encyclopedia* (now published by Encyclopedia Britannica).

In 1953, while returning with his family to duty with the U.S.D.A. in Nicaragua, Dr. Swain was ambushed en route and killed by bandits. With heroic courage and fortitude Su Zan with her two boys, then only ten and twelve years old, made her way back to the United States "to put together their shattered life." In Chatham, New Jersey she resumed her career as author and illustrator, producing in succession *Insects in their World* (1955), *Plants of Woodland and Wayside* (1958), and *First Guide to Insects* (1964) all published by Doubleday. She illustrated nature books and articles for many other authors and publishers, and has had her work exhibited in museums and galleries throughout the country, most recently in *The Five Noguchi Sisters Exhibit* in honor of Japanese-Americans, sponsored by the Arts Council of Sterling, Colorado. Her two sons have both attained distinction, Tom as an herpetologist and Ralph in the field of mass communications.

Elected in 1953 to Honorary Life Membership, Su Zan has contributed to the New York Entomological Society the cover design of its Journal as well as a memorable seminar on the history of entomological illustration, with examples from the rare book room of the American Museum of Natural History Library, and spiced with refreshments in the form of various edible insects. In the letter informing her of her election (four years earlier!) Dr. E. S. Hodgson, then Secretary of the Society wrote: "We know of no other person who has produced such consistently excellent drawings and paintings of insects and other natural history subjects. We greatly admire the combination of realism and scientific accuracy with sensitive artistry in your work."

In 1969 Su Zan was married to William Kenneth Firmage. Though nominally retired, both she and her husband continue active work, Su Zan in



Su Zan Swain Firmage at home in her study in Great Barrington, MA.

oils and wood carving. They travel widely, always returning to their summer home in Massachusetts or to their winter home in Florida.

Asher E. Treat
Tyringham, Massachusetts

OBSERVATIONS ON THE NESTING BEHAVIOR OF *TACHYTES*
TRICINCTUS (F.) ON SAN SALVADOR ISLAND, BAHAMAS
(HYMENOPTERA: SPHECIDAE, LARRINAE)

Nancy B. Elliott and Paul Salbert

Abstract.—Nesting females of *Tachytes tricinctus* (F.) were observed on San Salvador Island, Bahamas, during June, 1978. This paper reports the first published data on nest construction and predatory behavior in this species. Females captured acridid grasshoppers, *Ophullela pelidna pelidna* Burmeister and *Delia* sp., which were carried to the nest in flight. The nests were multicelled with one to five cells per nest; cells were located below the level of the main burrow, and contained two to nine prey. Evidence is presented that females of this species capture all the prey for a particular cell before ovipositing on one of the prey.

Introduction

Individuals of the genus *Tachytes* are large active solitary wasps. Typically females of this genus dig multicellular nests surrounded by distinctive circular mounds of soil (Evans and Kurczewski 1966). They provision these nests with Orthoptera from various families.

Bohart and Menke (1976) included *Tachytes tricinctus* (F.) in the *T. distinctus* species group, and reported its distribution to be the West Indies. In June, 1978, we observed a nesting aggregation of females on San Salvador Island, the Bahamas. Our observations, reported here, represent the first published information about nesting behavior in this species.

Results

We observed females nesting in a sparsely-vegetated area of hard-packed sand at the edge of an abandoned field adjacent to the old naval base now operated by the College Center of the Finger Lakes. While we did collect males of the species on San Salvador during the period of the study, none were seen at the study site. Twelve nests were observed in the area which represented a narrow strip, approximately 10 by 50 meters. Other species of digger wasps including *Cerceris zonata* Cresson and *Prionyx thomae* (F.) also nested in the area as did several ground-nesting bees. Our observations were made between 6 and 19 June 1978.

During collecting trips made to the island yearly in November through December since 1975, we have collected many sphecids, but never *T. tri-*

cinctus (Elliott et al. 1979). Therefore, we conclude this is a summer nesting species on the island.

Nest construction.—We found several burrows in the process of construction, but did not observe their actual beginning. These burrows were closed and were marked by large spoil heaps, indicating extensive digging within. One nest, first observed at 1415 hours on June 15, was noted open the next day at 828 hours.

Orientation.—A female about to leave her nest to hunt for prey, walked out of the entry onto the spoil heap. She then took flight, hovering above the nest, facing the entry and flying in successively wider and higher circles around the nest. Orientation lasted a total of ten seconds. The female then flew away to hunt, leaving the burrow open.

Predatory behavior.—Females were often away from the nests for several hours hunting for prey. The prey, always acridid grasshoppers, were carried to the nest in flight. Typically the burrow was open, and the female entered directly carrying her prey. One female, returning to a nest that had accidentally been covered in her absence, was seen holding her prey with all three pairs of legs as she approached. Then, supporting herself with the middle legs, and holding the prey with the hind legs, she used the mandibles and forelegs to dig at the closed entrance. Eventually she released the prey to dig, but soon retrieved it.

Another female, encountering a grasshopper inside an insect net, stung it and prepared it for carriage. She grasped the antennae with her mandibles and turned it sideways under her body, preparing it for transport. This grasshopper, however, was larger than any we saw females carry to the nest. It weighed 240 mg, and all prey weighed averaged only 93.8 mg. Hence the mounting behavior observed may have been atypical.

Two species of acridids were used as prey. They were *Ophulella pelidna pelidna* (Burmeister) and *Delia* sp. They ranged in weight from 36.3 mg to 214 mg ($n = 13$; $\bar{x} = 93.8$ mg). Females capturing the prey ranged in weight from 110 mg to 133 mg ($n = 5$; $\bar{x} = 126.5$). The mean ratio of weight of prey to weight of wasp carrying it was .75 ($n = 12$; range = .33–1.61). We noted a slight tendency for females to take larger grasshoppers later in the period of our study, and this seemed to indicate that females simply captured those individuals of suitable species available, thus taking larger grasshoppers as the prey species matured. A similar tendency was observed in *T. crassus* Patton by Evans and Kurczewski (1966).

Nest characteristics.—Eleven nests were excavated and reconstructed using the methods described by Salbert and Elliott (1979). Table 1 summarizes the important nest and cell characteristics we quantified. The entries of relatively new nests were surrounded by circular mounds of soil. These were abraded or completely absent at older nests. The shape of each entry burrow depended on the substrate and might deviate from the vertical if

Table 1. Nest and cell characteristics of *Tachytes tricornatus* (F.).

Characteristic	Mean	Range	Number
Diameter of spoil heap	7.5 cm	6.5–10.5 cm	9
Height of spoil heap	3.3 cm	2.7–3.5 cm	4
Maximum depth of burrow	14.5 cm	2.5–19.0 cm	11
Depth of cells	20.3 cm	7–29.0 cm	42
Number cells/nest*	2.6	1–5	8
Length of cell	2.9 cm	1.7–4.0 cm	8
Width of cell	1.2 cm	0.6–2.0 cm	7
Height of cell	1.2 cm	1.0–1.5 cm	5
Prey/cell (when whole)	4.2	2–9	4
Length of cocoon (when present)	1.5 cm	1.2–1.7 cm	6

* An older nest which contained 21 cells, many of them already empty has not been included in this measurement.

bypassing a rock. While many nests had nearly vertical burrows, one ran vertically for about 11 cm; then it became nearly horizontal. The soil below the level of this particular burrow was very rocky. The cells were located at or below the level of the main burrow. With a single exception, all cells had been closed off from the main burrow. One old nest, associated with three entrance holes, contained 21 cells, many of them bearing evidence that their occupants had already emerged. Newer nests contained from one to five cells. The cells with whole prey contained from two to nine grasshoppers. All prey, for which placement could be determined, were placed in the cell with the head inward, but varied as to whether they had been placed venter up or on their sides.

Nest closure.—The females closed their nests at night and sometimes during midday. A female preparing to leave the nest in the morning, removed the sand closure with her mandibles. Possibly sand is pushed into the entry to form the closure as a result of additional digging going on within the nest.

Discussion

In general our observations on the nesting behavior of *Tachytes tricornatus* agree with those made by Williams (1913) on its North American relative, *T. distinctus* Smith, and those summarized by Bohart and Menke (1976) for all species of the *Tachytes distinctus* species group. The females of these species all prey on acridids, which are carried to the nest in flight, and construct multicellular nests with one to several prey per cell.

A few reports indicate that females of *Tachytes validus* must capture all the prey to be used in a particular cell before ovipositing (Evans and Kurczewski 1966; Kurczewski and Ginsburg 1971). Our observations indicate

that this may also be the case for *T. tricinctus*. In one excavation we found a single acridid in the burrow about 2.5 cm from the open cell. The cell itself contained two more fresh grasshoppers, but no egg. We had captured the female returning with prey late in the afternoon. Presumably the grasshopper in the burrow and the one she was carrying would also have been placed in the open cell. Evans and Kurczewski (1966) reported that females of *T. validus* stored prey for a particular cell in a separate pocket of the nest prior to oviposition. Perhaps females of *T. tricinctus* leave prey in the burrow for the same reason.

Acknowledgments

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Dr. Ashley B. Gurney, U.S.D.A. Systematic Entomology Laboratory, determined the prey.

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Department of Biology, Hartwick College, Oneonta, New York 13820.

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LIFE HISTORY, MORPHOLOGY, AND TAXONOMY OF *ACUTALIS*
TARTAREA (SAY) (HOMOPTERA: MEMBRACIDAE)¹

James H. Tsai and Dennis D. Kopp

Abstract.—*Acutalis tartarea* (Say) is a membracid species found throughout the northeastern $\frac{2}{3}$ of North America. We present information on its biology and field life history in Florida and draw comparisons with the biology of *Micrutalis malleifera* (Fowler).

A discussion of the polymorphic forms of *A. tartarea* is presented along with the reasoning for suppression of the names *Acutalis semicrema* (Say) and *Acutalis inornata* (Ball), both of which are color polymorphs. The immature stages of *A. tartarea* are described and illustrated.

Acutalis tartarea (Say) and closely related *Micrutalis* spp. were found in rotary flight traps near and on the undergrowths of coconut plantings during a study of homopterous insects associated with lethal yellowing (LY) disease of coconut palms in Florida (Tsai 1980). Simons and Coe (1958) found the treehopper *Micrutalis malleifera* (Fowler) to be the vector of pseudocurly top virus (PCTV) in tomatoes grown in Florida. Their work provided the first documented record of a treehopper vector of a virus disease.

In light of Simons and Coe's work, *A. tartarea* was considered a possible vector of LY due to its proximity to diseased trees. Since little was known of its biology and life history the following study ensued. The purpose of this paper is to report on the life history, morphology, and taxonomic status of *A. tartarea*.

Materials and Methods

Since common ragweed (*Ambrosia artemisiifolia* L.) was found to be a natural host of *A. tartarea* in the field, it was the principal host plant in laboratory rearings. Seedlings were transplanted to styrofoam pots *ca.* 5 cm in diameter and held in a greenhouse equipped with an evaporative cooling system that maintained a temperature at *ca.* 27°C. Relative humidity was not controlled. China aster (*Callistephus chinensis* (L.) Nees), eggplant (*Solanum melongena* L.) and periwinkle (*Catharanthus roseus* (L.) G. Don) also were used for life history studies in the laboratory, under the same conditions as common ragweeds.

A. tartarea adults were collected in the Fort Lauderdale area to establish

¹ Florida Agricultural Experiment Station Journal Series No. 2346.

laboratory colonies. The stock colony of *A. tartarea* was reared on common ragweed in a rearing room at $24 \pm 1^\circ\text{C}$ and R.H. $75 \pm 5\%$. Light intensities of 7,000 lux were provided by a bank of six fluorescent lights with a 12 hour photophase and 12 hour scotophase. The same conditions were provided for life cycle study.

In order to study nymphal development, host plants were modified by trimming the excess foliage from the terminal tips and placing these trimmed tips in rearing cages. Rearing cages consisted of 4.5 cm plastic petri dishes with their sides notched to accept the terminal stem of the host plant. The portion of the stems which passed through the notch in the petri dish was wrapped with sponge rubber to form a tight seal and prevent escapes. Dark colored paper was placed on the bottom of the dish to facilitate the observation of molted skins. Ventilation was provided by cutting a small hole in the petri dish lid and glueing a fine screen over it. Daily observations were made on each rearing cage throughout the duration of the study.

The morphological characters of each life stage were described and illustrated with the aid of a camera lucida mounted on a Wild® 5M dissecting microscope at $25\times$ magnification. Measurements of nymphs in each instar were made with a Bausch and Lomb Zoom 7 Stereoscope® and a calibrated ocular micrometer.²

Results

Laboratory Life History Studies and Field Observations.—*A. tartarea* eggs hatch and the nymphs pass through 5 instars before moulting into the adult. Adult females generally lay eggs in clusters of 12–15 eggs each. These eggs are inserted into the epidermal tissue of the host plant which has been slit by the female ovipositor. Eggs are inserted to a depth that leaves *ca.* $\frac{1}{3}$ of the egg exposed. Of the 82 plants examined, the favored oviposition sites were in the axis area of the leaf (70%) and the stem terminus (27%). Approximately 3% of the time, eggs were found completely exposed and held by the dense epidermal hairs of the host plant. On common ragweed, the number of eggs laid by a single female ranged from 12 to 62 and incubation time ranged from 10–23 days with a mean of 15.7 ± 3.2 (S.D.) days. On aster incubation time was significantly longer ($t = 2.72$, $df = 38$, $P = 0.01$) (see Table 1).

Early instar nymphs exhibit gregarious, sedentary behavior near the terminal portion of the ragweed plant. Early instars remain in the area of egg hatch and, as nymphal development progresses, later instar nymphs dis-

² ® The use of a trademark name is not an endorsement of one product over another that is equally effective.

Table 1. Developmental time (in days) of *Acutalis tartarea* (Say) reared on common ragweed (*Ambrosia artemisiifolia* L.) and China aster (*Callistephus chinensis* (L.) Nees at $24 \pm 1^\circ\text{C}$.

Life stage	Common ragweed				China Aster			
	Sample size	Mean	Range	S.D.	Sample size	Mean	Range	S.D.
Egg	24	15.7	10-23	± 3.2	16	19.5	15-26	± 3.1
1st Instar	22	4.5	3-8	± 1.9	12	9.2	8-11	± 0.9
2nd Instar	22	5.5	3-10	± 1.5	11	9.6	7-12	± 1.9
3rd Instar	22	4.5	3-7	± 1.7	9	10.4	8-13	± 1.6
4th Instar	17	6.6	4-11	± 2.1	14*	12.0	10-15	± 1.5
5th Instar	15	12.1	7-30	± 3.1	13	13.0	10-16	± 2.1
Total mean development time		49.9				73.7		
Adult longevity								
Female	14	12.1	3-45	± 4.1	9	32.0	8-55	± 6.4
Male	21	7.9	1-30	± 3.1	7	20.0	7-31	± 5.6

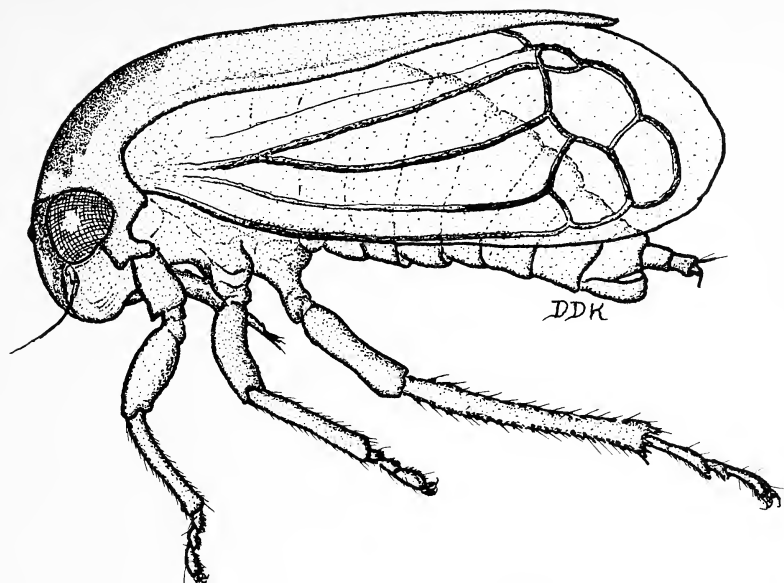
* Due to the increasing mortality, insects were supplemented by individuals from the colony reared on China aster. Their ages were determined on the basis of wing-pad development.

perse on the plant. Nymphal feeding occurs on the stems and petioles with individuals maintaining a head down stance. No feeding was observed on the leaves.

When reared on common ragweed, the mean nymphal development time for the 5 nymphal instars was 34.2 days at $24 \pm 1^\circ\text{C}$ (see Table 1). The mean time of nymphal development for instars 1 through 4 was between 4-6 days each and that for the 5th instar was about twice that of the earlier instars on common ragweed. Nymphs reared on aster have a longer developmental time ($t = 2.62$, $df = 155$, $P = 0.01$) (see Table 1).

Laboratory reared male and female adults live significantly longer ($t = 2.73$, $df = 33$, $P = 0.01$; $t = 2.98$, $df = 14$, $P = 0.01$ respectively) on China aster host than on common ragweed. On both hosts, female longevity is greater ($t = 2.83$, $df = 21$, $P = 0.01$; $t = 2.78$, $df = 26$, $P = 0.01$ respectively) than that of the male (see Table 1). Rearings were also attempted using eggplant (*Solanum melongena* L.) and periwinkle (*Catharanthus roseus* (L.) G. Don) but *A. tartarea* could not survive on either of these hosts.

Field observations substantiated egg cluster size, oviposition site selection, nymphal behavior and nymphal feeding orientation. Adult flight activity in the field occurred after 9:00 a.m., this seemed to be related to temperature and possibly light intensity. Greatest flight activity occurred during the warmest portions of the day. The most common field host of *A. tartarea* in Florida was common ragweed but the species was occasionally found on *Bidens bipinnata* L. (Spanish needles).



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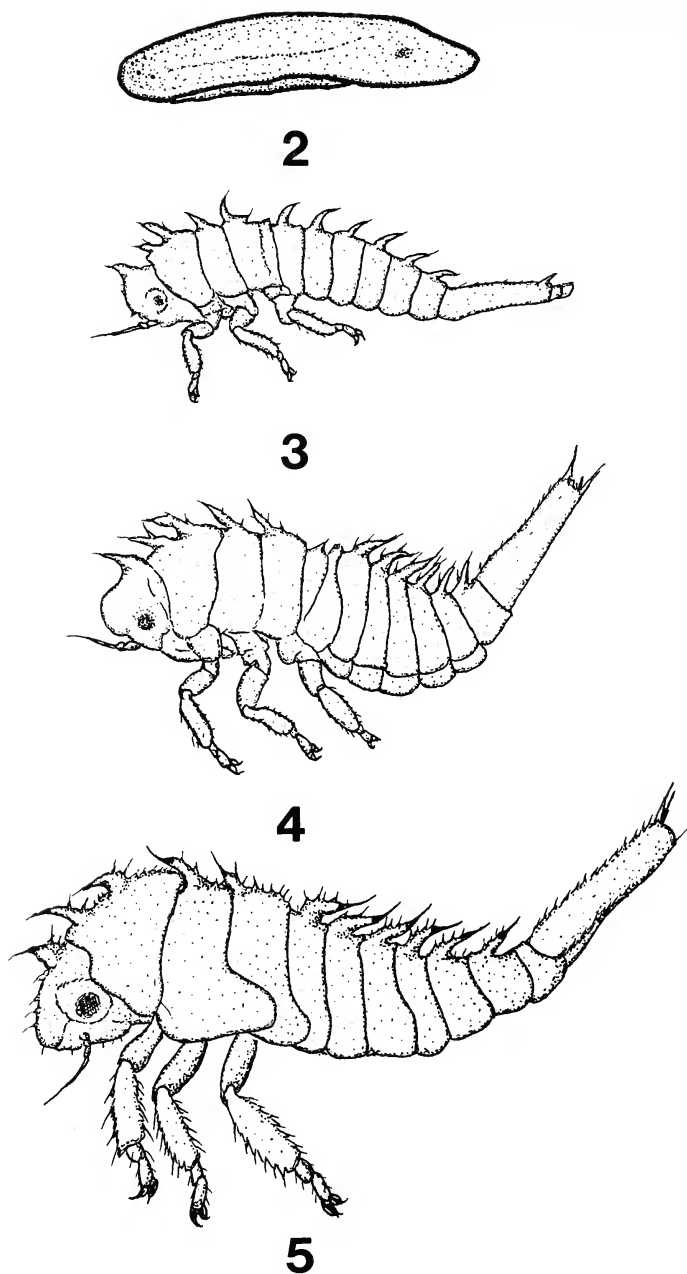
Fig. 1. Lateral view of adult male *Acutalis tartarea* (Say).

A monthly population survey was made from May 1978 to April 1979 by visually counting all *A. tartarea* on 35 ragweed plants randomly selected in the field (Fig. 8). The population was at very low levels from August through November. During this period the growth of ragweed in the field was greatly affected by environmental factors such as high temperature, dry months, and long day length.

Morphology

Adult.—The adult *A. tartarea* (Fig. 1) possesses the typical characteristics of Subfamily Smiliinae with its prothoracic tibiae not foliaceous, its metathoracic tarsi equal in size to the prothoracic and mesothoracic tarsi, three longitudinal veins in the tegmen arising near the base of the forewing and five apical cells present in the forewing. The head is twice as broad as long and the pronotum extends beyond the abdomen, but not covering the tegmen. The colors of the head, pronotum tegmen and legs vary from green to black. The adult female is 3.7 ± 0.07 mm (range: 3.5–3.9 mm) in length and 1.9 ± 0.00 mm (range: 1.8–1.9 mm) in width. The male is 3.3 ± 0.09 mm (range: 2.8–3.4 mm) long and 1.7 ± 0.03 mm (range: 1.5–1.9 mm) wide.

Since the immature stages of this species have not been previously de-



Figs. 2-5. 2. Side view of egg of *Acutalis tartarea* (Say). 3. Lateral view of 1st instar nymph of *A. tartarea*. 4. Lateral view of 2nd instar nymph of *A. tartarea*. 5. Lateral view of 3rd instar nymph of *A. tartarea*.

scribed or illustrated in the literature, their description and measurements are presented below.

Egg (Fig. 2).—Mean length 1.0 ± 0.02 mm (range: 0.9–1.1 mm), width 0.3 ± 0.00 mm (range: 0.2–0.3 mm). Color white and translucent with one end blunt and the other end pointed.

First Instar (Fig. 3).—Mean length 1.4 ± 0.03 mm (range: 1.1–1.6 mm), width 0.3 ± 0.00 mm (range: 0.3–0.4 mm). Color pale green. Dorsum bearing well developed paired spines, 1 pair anterior projecting from vertex of head, 2 pair anterior projecting from dorsum of prothorax, 1 pair anterior projecting from dorsum of mesothorax. One posterior projecting pair from dorsum of metathorax and posterior projecting pairs from dorsum of abdominal segments 3, 4, 5, 6, 7, and 8.

Head: Clypeus triangular and hirsute; eyes prominent, projecting laterally, pigmented red. Vertex bearing 1 pair of well developed anterior projecting spines; rostrum projected caudad between prothoracic legs to metacoxae. Antenna located in front of eye, basal 3 segments enlarged and terminal segments filamentous.

Thorax: Dorsum of prothorax bearing 2 pairs of anterior projecting spines, one on either side of median line; 1 pair of anterior projecting spines on dorsum of mesothorax; 1 pair of posterior projecting spines on dorsum of metathorax. Pro, meso and metacoxae well developed; femora sparsely hirsute; pro and mesotibiae laterally compressed and expanded with setae on lateral edges; metatibiae $\frac{1}{3}$ longer than pro and mesotibiae, only slightly compressed; tarsi 2 segmented, tarsal claws swollen at base.

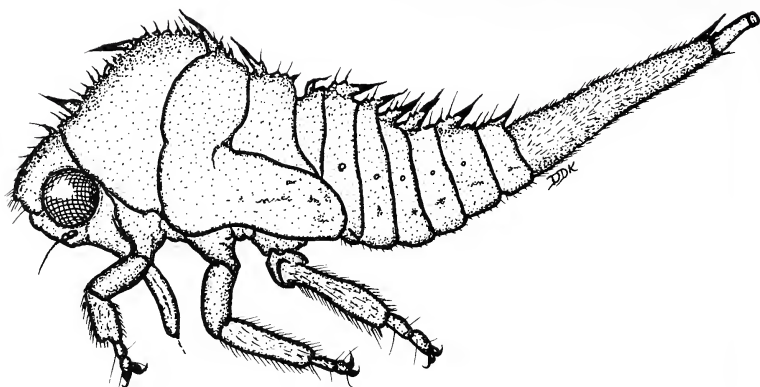
Abdomen: Dorsum of abdominal segments 1 and 2 unarmed, compressed against mesothorax, segments 3–8 each armed with a pair of posterior projecting dorsal spines, one on either side of median line; venter of segments 1–8 convex and with prominent setae; segment 9 elongate, tapering to apex, subequal in length to combined length of segments 5–8; segment 9 bearing a dorsal pair of posterior projecting spines, entire segment setaceous.

Second Instar (Fig. 4).—Outline and shape similar to previous instar, except in size. Mean length 1.8 ± 0.05 mm (range: 1.6–2.1 mm), width 0.5 ± 0.01 mm (range: 0.4–0.7 mm). Color pale green. Paired dorsal spines on either side of median line bearing secondary lateral setae.

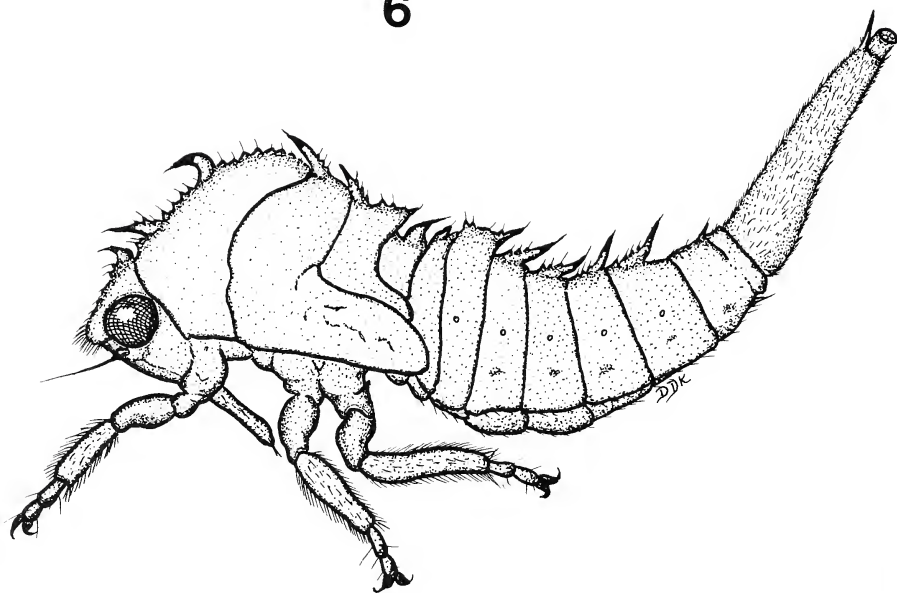
Head: Similar to previous instar in outline and shape. Dense setae on clypeus, frons and vertex.

Thorax: Paired dorsal spines with secondary setae on dorsal edge, tips fuscous. All paired dorsal thoracic spines projecting anteriorly. Pro and mesothoracic legs similar in form and size, tibiae laterally compressed, dense setae on margins. Tibiae of metathoracic legs triangular in cross section, $1\frac{1}{2}$ times length of pro and mesothoracic tibiae.

Abdomen: Dorsum of abdominal segments 1 and 2 with short, prominent



6



7

Figs. 6, 7. 6. Lateral view of 4th instar nymph of *Acutalis tartarea* (Say). 7. Lateral view of 5th instar of *A. tartarea*.

setae. Dorsum of segments 3, 4, 5, 6, 7 and 8 with prominent posteriorly projecting spines, spines with secondary setae on dorsal margin. Abdomen triangular in cross section, folding along line of junction of the lateral and ventral plates. Segment 9 elongate, tapering to apex.

Third Instar (Fig. 5).—Outline and shape similar to previous instar except in size and caudal edge of the meso and metathoracic lateral plates developed into wing buds. Mean length 2.6 ± 0.10 mm (range: 2.0–2.8 mm), width 0.7 ± 0.05 mm (range: 0.5–0.8 mm). Color pale green. Paired dorsal spines on head, thorax and abdomen with tips black. Venter of abdomen concave.

Head: Frons densely covered with setae, caudal edge of clypeus forming a ridge between eyes.

Thorax: Similar to previous instar except wing buds apparent on meso and metathoracic segments. Mesothoracic wing buds covering $\frac{1}{2}$ of metathoracic wing buds. Metathoracic wing buds covering $\frac{1}{2}$ of 3rd abdominal segment.

Abdomen: Abdominal segments 1 and 2 covered by caudal edge of metathoracic plate. Venter of abdominal segments concave. Segment 9 elongate, tapering to apex.

Fourth Instar (Fig. 6).—Outline and shape similar to previous instar except in size. Mean length 3.3 ± 0.15 mm (range: 2.5–3.9 mm), width 0.9 ± 0.04 mm (range: 0.7–1.1 mm). Color pale green. Mesothoracic wing buds extending onto 3rd abdominal segment. Metathoracic wing buds well developed and covered by mesothoracic wing buds. Paired dorsal spines prominent, with black tips. Venter of abdomen strongly concave.

Head: Setae dense on clypeus and frons. Paired dorsal spines on vertex smaller than thoracic or abdominal dorsal spines.

Thorax: Prothoracic dorsal sclerite extending caudo-mesad over $\frac{1}{2}$ of metathoracic dorsum between paired dorsal spines. Mesothoracic wing buds covering metathoracic wing buds and extending onto 3rd abdominal segment.

Abdomen: Venter of abdomen strongly concave. Segment 9 elongate, tapering to apex and subequal to the combined length of segments 2–8.

Fifth Instar (Fig. 7).—Outline and shape similar to previous instar except in size. Mean length 5.7 ± 0.21 mm (range: 3.3–7.7 mm), width 1.3 ± 0.10 mm (range 0.8–1.8 mm). Color pale green. Body setae dense. Paired dorsal spines on head, thorax and abdomen with prominent black tips. Venter of abdomen strongly concave.

Head: Setae dense on clypeus and frons. Paired dorsal spines on vertex $\frac{1}{3}$ to $\frac{1}{2}$ length of thoracic and abdominal dorsal spines.

Thorax: Prothoracic dorsal sclerite extending between paired dorsal

spines of mesothorax. Mesothoracic wing buds covering metathoracic wing buds and extending caudally onto 3rd abdominal segment.

Abdomen: Venter strongly concave.

Taxonomy

In America, north of Mexico, the genus *Acutalis* historically has had three described species: *A. tartarea* (Say), *Acutalis semicrema* (Say) and *Acutalis inornata* (Ball). Differentiation of these three species was based upon coloration of the pronotum and pigmentation of the venation of the tegmen (Van Duzee 1908). *A. tartarea* was the darkest in coloration and this traditionally has been applied to specimens collected throughout the Northeast, North Central and West Central portions of North America. *A. semicrema*, originally described from Florida material, was not as darkly pigmented as *A. tartarea*. More recent distribution records show the range of *A. semicrema* to be very similar to that of *A. tartarea*. *A. inornata*, described by Ball (1905) from Florida, is entirely green in color with no black markings. Most distribution records of *A. inornata* have been from Florida. However, intensive collecting in more northern states has produced specimens that would be classified as *A. inornata* (Kopp and Yonke 1973).

As early as Matusch (1912) field observations were casting doubt upon the species status of *A. tartarea* and *A. semicrema*. His observations indicated that many of the females in his New Jersey collecting site were of the *A. semicrema* form while the males were of the *A. tartarea* form. This also was observed by the authors, who view this coloration pattern as a form of sexual dimorphism.

Caldwell (1949) studied the genitalia of the three described species of *Acutalis* and could not find distinctive differences. He treated these three forms as trinomials, *Acutalis tartarea tartarea* (Say), *Acutalis tartarea semicrema* (Say) and *Acutalis tartarea inornata* (Ball). From Caldwell's treatment it is apparent he used the trinomial to designate color varieties of the same species, not, as today, to denote subspecies.

We feel that Caldwell's treatment of these three species as one is entirely justified. We view *A. tartarea* as a single species that in the adult stage presents several different polymorphic color forms to the environment. Intensive collecting of local populations in Missouri and Florida has produced representatives of all three forms.

Field observations of populations in Florida offer another line of evidence for the acceptance of the single species with several color morphs. In Florida, where the three morphs can be most frequently encountered, mating between the forms has been observed from February to June. These matings in the natural habitat are strong evidence indicating a lack of reproductive isolation necessary for species consideration of each form. No infertility

was observed in the laboratory studies in which 9 pairs of green and black forms were crossed. Of the 152 individuals produced, 40 of the green forms were found to be female, and 86 of the black-headed forms were males.

The following listed synonymy is presented for the species *Acutalis tartarea* (Say).

Micrutalis tartarea Say, 1830:242:1.

Micrutalis semicrea Say, 1830:242:2.

Acutalis anticonigra Fairmaire, 1846:498.

Tragopa brunnea Provancher, 1872:320.

Acutalis inornata Ball, 1905:119.

Acutalis tartarea semicrema Van Duzee, 1917:529.

Acutalis tartarea tartarea Severin, 1927:33.

Acutalis tartarea inornata Caldwell, 1949:498.

Acutalis tartarea semicrema Caldwell, 1949:498.

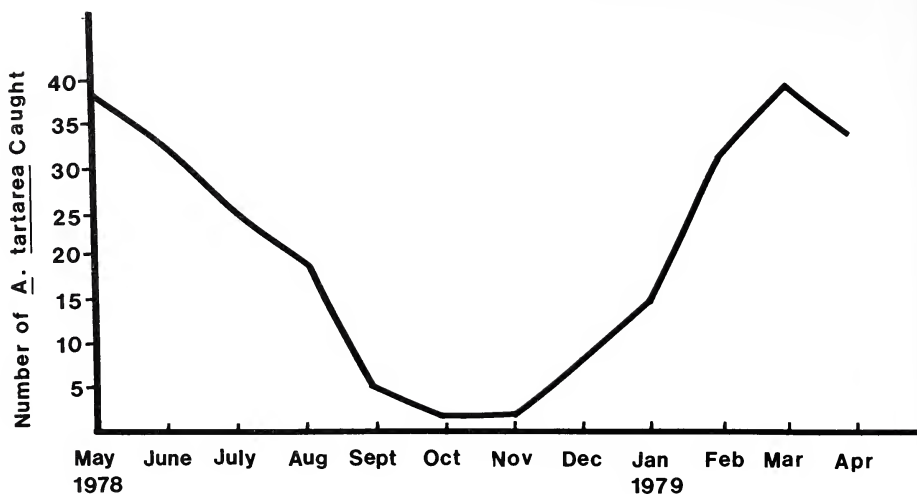
Discussion

A. tartarea has a broad range and presents a variety of color polymorphs within populations. Three of these polymorphs have been described as species, traditionally separated from each other by their colors and patterns of coloration. Matusch (1912) doubted the validity of species status for both *A. tartarea* and *A. semicrema* based on field observations in New Jersey. Caldwell's (1949) studies on the insect's genitalia indicated that there was a single species of *Acutalis* in America, north of Mexico, and he listed the polymorphs as varieties of *A. tartarea*.

Field observations by the present authors indicate that many populations had 2 or more polymorphs present which freely interbreed in nature, thus supporting the observations of Matusch (1912). Laboratory rearings were accomplished with several polymorphs and no abnormal infertility was observed.

We view *A. tartarea* as a single species with color polymorphs throughout its range. These morphs show different proportions in different geographic areas. The biological mechanism of expression of these polymorphs is not understood but may be a complex interrelationship of ecotypical color forms, temperature related color expression, sexual dimorphism, and/or a nymphal host plant relationship. Further autecological studies will be required to fully understand these forms.

Our observations on the life history of *A. tartarea* shows similarities to the life history of *M. malleifera* as observed by Simons (1962). These similarities are: mean incubation time of the eggs, mean development time of instars 1 to 3, presence of adults in the field year round in Florida, gregarious behavior of early instar nymphs, head down feeding stance of the nymphs



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Fig. 8. Monthly total numbers of adults and nymphs of *Acutalis tartarea* (Say) found on common ragweed.

and highest reproductive activity during the active growing seasons of their respective hosts.

A. tartarea has 5 nymphal instars with a total mean development time from egg to adult of about 50 days. This is about 25% longer than *M. malleifera*. Simons (1962) indicated *M. malleifera* had 4 nymphal instars, which is remarkably unusual since all other treehoppers, whose biology have been studied, have 5 nymphal instars. The difference may have been due to rearing hosts (Simons, personal communication).

In Florida populations of both *A. tartarea* and *M. malleifera* show fluctuation trends through the season. Both species are most active and reach highest populations during the warmest months. Lowest field populations of *M. malleifera* occur from October through April (Simons 1962). Populations of *A. tartarea* show rapid decreases during July, reaching a low during the months of August through November (Fig. 8). Seasonal population fluctuations of both species are related to the seasonal growth cycle of their host plants.

The favored field host of *A. tartarea* in Florida is common ragweed. Laboratory rearings on this host were quite successful. China aster was also used as a laboratory rearing host for *A. tartarea*. The species could be continuously reared on this host but individuals reared on it showed longer development time than those reared on common ragweed (see Table 1). It was also noted that adults of *A. tartarea* which had been reared from the

egg stage on China aster, had a greater adult longevity than those reared on its native host plant.

Acknowledgment

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(JHT) Agricultural Research Center, University of Florida, 3205 S. W. 70th Avenue, Fort Lauderdale, Florida 33314 and (DDK) Cooperative Extension Service Agriculture and Applied Science, North Dakota State University, Fargo, North Dakota 58105.

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ECOLOGY OF NECROPHILOUS AND CARPOPHILOUS
COLEOPTERA IN A SOUTHERN NEW YORK
WOODLAND. PART I—OVERVIEW¹

Dominick J. Pirone² and Daniel J. Sullivan, S.J.³

Abstract.—Almost 20,000 individual Coleoptera were collected, pinned and labeled from 6 pitfall traps baited with decomposing smelt fish to attract necrophilous beetles, and 6 traps baited with decaying cantaloupe melon for carpophilous species. Six of these traps (3 pairs with each type of bait) were located on a dry slope, and 6 others in an adjacent wet valley. This field sampling was done over an 8-month period (April thru November) at Fordham University's Calder Ecology Center, Armonk, Westchester County, New York. Approximately equal numbers of beetles were taken from each bait (fish and melon), and from each habitat (slope and valley). The trapped Coleoptera were concentrated in 10 major Families (99.4%), plus 5 minor Families (0.4%) and 18 adventitious Families (0.2%). These 10 major Families also comprised 76.5% of the total 217 species trapped. The 3 most numerous Families were the Staphylinidae (37.1%), Silphidae (21.5%) and Nitidulidae (17.9%). These were followed by the Hydrophilidae (7.1%), Lep-todiridae (4.9%), Histeridae (3.4%), Carabidae (2.3%), Ptiliidae (2.0%), Scarabaeidae (1.9%), Scolytidae (1.3%). Certain species were consistently attracted to fish (necrophilous) and others to melon (carpophilous). However, in both cases, many of the beetles are actually predatory, and some are general scavengers. Closely related species are usually separated temporally, most often by fortnightly periods. The geography, geology and botany of the research area are discussed as representing a southern New York woodland situated less than 50 k north of midtown Manhattan.

Introduction

The purpose of this research was to identify and enumerate the families, species and individuals of necrophilous and carpophilous Coleoptera collected at traps baited with decaying fish and melon. The field study was done in 2 ecologically distinct but adjacent areas: a dry slope and a moist

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² Assistant Professor in the Department of Biology, Manhattan College, Riverdale, New York 10471.

³ Associate Professor in the Department of Biological Sciences, Fordham University, Bronx, New York 10458.

valley in an open woodland in southern New York State. The sampling collections were made over an 8-month period from April thru November.

Decaying carrion and fruit are an important food source for many species of insect larvae and adults, especially Diptera and Coleoptera. Beetles are always of particular interest because of their sheer numbers (perhaps 300,000 species) which comprise about $\frac{1}{3}$ of the world's known insect species. In addition, their well-known niche-specialization provides opportunities for remarkable diversity. For these reasons, Coleoptera can be studied to record food preferences between such energy sources as decaying fish and melon. Further comparisons can then be made in relation to habitat differences between a dry slope and a moist valley.

Therefore, these data were used to tabulate: (a) both the numerical and temporal relations between the species; (b) the food preferences for fish or melon; (c) the habitat association of the slope and valley. Such quantitative information concerning the relative proportions and preferences of ecologically related species should be continually added to the insect ecological literature (Matthews and Matthews 1970, Wallace 1974). Other authors such as Arnett (1970) caution further that it is not enough to know only the orders and families that occur in such habitats and have certain food preferences—but also that the species themselves, their population fluctuations and phenology must be studied. It is hoped, therefore, that the research presented here will provide basic information for use in taxonomic catalogs and future ecological studies. This *Part I* contains a summary overview of the entire project at the family level.

Materials and Methods

Field study.—The field work was done at Fordham University's Calder Ecology Center, Whippoorwill Road, Armonk, Westchester County, New York 10504. This sampling aspect of the research was conducted over an 8-month period from April thru November 1970. The field study area was 2.5 hectares, and was located in the northwest part of the 45 hectare Fordham Ecology Center. It consisted of 2 distinct but adjacent sections: a wide, western-exposed slope; a flat, narrower, stream-laced valley at the base of the slope and 27.4 m lower in altitude.

Geography, geology and pedology.—The Fordham Ecology Center is located 48.3 k north of midtown Manhattan in the County of Westchester, and ranges from 145–200 m above sea level. It is underlain by the Manhattan Prong of the igneous, highly metamorphosed Fordham Gneiss of the New England Upland (Muller 1965, Schuberth 1968), and may be of proterozoic (Precambrian) age, ca. 1 billion years old. It is about 56 k north of the southernmost terminus of the last Wisconsin glaciation which began receding about 15,000 years ago. This Fordham property is composed of the

Hollis association of soils (laid down on glacial till). It is a shallow, sandy loam 25–50 cm to bedrock, and slightly acidic, low in nitrogen and calcium, marginal in phosphorous, but adequate in potassium for tree growth. The slope is dry with shallow soil, while the valley is wet.

Botany.—The flora of the slope in this open woodland setting is dominated by typical beech (*Fagus grandifolia* Ehrhart), birch (*Betula lenta* L.) and red maple (*Acer rubrum* L.). The main associated trees are rock-chestnut oak (*Quercus prinus* L.), black oak (*Q. velutina* Lamarck) and red oak (*Q. rubra* L.). The shrub understory is composed of maple-leaved viburnum (*Viburnum acerifolium* L.), blueberries (*Vaccinium* spp.), pinxter-flower (*Rhododendron nudiflorum* Torrey), and mountain laurel (*Kalmia latifolia* L.). Some common vines, herbs, ferns, club-mosses and true mosses complete the list of the slope macrophytes.

In the valley, however, only infrequently are beech and birch found (limited to high spots), while the red maple, so common on the slope, is completely replaced by sugar maple (*Acer saccharum* Marshall). The oaks are entirely absent, perhaps because of the moist, deeper soil of the lower valley. Hence, the characteristic trees of the valley are the white ash (*Fraxinus americana* L.), black ash (*F. nigra* Marshall), bitternut hickory (*Carya cordiformis* Koch), mockernut hickory (*C. tomentosa* Nuttall), and tulip-poplar (*Liriodendron tulipifera* L.). Witch-hazel (*Hamamelis virginiana* L.) is usually a somewhat isolated species elsewhere, but in the valley it is common and attains a large size and extensive coverage. Spicebush (*Lindera benzoin* Blume) dominates the high shrub layer. It is in the herbaceous strata, however, that the well-watered valley differs very strongly from the drier slope. The darker, deeper valley soil supports a nearly continuous carpet of lush herbaceous growth, ranging from just above ground level to over 1 m in height.

In summary, the total number of macrophyte species for each of the 2 study areas was: slope 29 and valley 78, with many species common to both. By combining the total species for both slope and valley, a breakdown of the above data reveals that there was a total of 22 species of trees; 17 shrubs and woody vines; 47 herbs, woodrush, grasses; 13 species of ferns, clubmosses and true mosses.

Meteorology.—The Fordham Ecology Center is located just inside the southern boundary of the climatic division of New York State known as the "Hudson Valley." The annual normal temperature for the study area is about 11°C. The temperatures on the slope ranged from a high of 32°C on the early date of May 10th to a low of -21°C on January 22nd. In the valley, a similar pattern was recorded, but usually 2.24°C lower in each case. The highest temperatures each day were reached between 1–3 PM, while the lowest were between 4–7 AM.

On days without precipitation, the relative humidity in the valley was

usually 5–10% higher than that of the slope. The precipitation is about 112 cm annually, and well-distributed throughout the year, with a fairly regular monthly average of slightly over 8.9 cm. During 1970, however, only 75 cm fell in the study area.

Traps.—Each of the 12 pitfall bait traps consisted of a 3.78 l cylindrical tin can (size no. 10). In order to allow for rain and runoff water drainage, 25 tiny nail holes were hammered into the bottom of each trap in a regular pattern. A hole was dug for each trap so that the rim of the can was exactly flush with the surrounding woodland floor substrate. The outer circumference of each trap was packed with soil so that no intervening gaps remained. A .47 l uncoated cardboard container was placed inside each trap to hold the bait. A 23 × 23 cm square of galvanized 1.3 cm hardware screen was placed on top of each trap. Four 2.0 cm thick small stones were placed at each of the 4 corners of the screen to permit a crawl-space for the anticipated beetles to enter the trap. This in turn was covered by a 23 × 23 cm square piece of 0.6 cm masonry hardboard which acted as a rain-shield. Finally, in order to protect the pitfall trap from racoons and other bait-raiders, a large, heavy rock was placed over each rain-shield.

Bait.—Six traps were baited with fresh cantaloupe melon (*Cucumis melo* L.), sliced into sixths and the seeds removed. On the 1st day of baiting, 2 of the slices were placed in the cardboard container. On the 2nd day of collecting and replacement of the bait, 1 of the 2 slices of melon was removed from the trap and replaced by a fresh piece. Hence, a cyclic regimen was maintained so that 1 slice of melon was usually 0–3 days old, and the other slice 4–7 days old in each of the 6 melon traps.

The 2nd set of 6 traps was baited with 2 frozen, whole (18–23 cm) Atlantic smelt (*Osmerus mordax* Mitchell) with viscera and all body parts left intact. The same regimen was followed in baiting with fish as with melon, so that 2 fish in different stages of decomposition were always in each bait container.

Three melon and 3 fish pitfall traps were located on the slope, and an equal number in the valley area. These 12 traps were placed in pairs (1 melon–1 fish) at approximately 12 m distance from each other. These pairs in turn were located 24 m apart.

Collections were made from the traps twice weekly (3–4 days apart) between 1–7 PM, during the 8-month study period. The removed bait was carefully dissected in an aluminum baking pan in the field in order to insure collection of all specimens which had bored into the bait (usually nitidulids and scolytids). Other beetles were removed directly from the bait containers, and put together with the aforementioned Coleoptera into 57 g screw-top labeled jars containing 80% ethyl alcohol mixed with 2% glycerine by volume. Each area was sampled 46 times for a total of 552 separate collections.

Table 1. Families of Coleoptera collected from traps baited with fish for necrophilous beetles and melon for carpophilous species over an 8-month period (April thru November) at Fordham University's Calder Ecology Center, Armonk, Westchester Co., N.Y.

Family	Individuals		Species	
	No.	%	No.	%
1. Staphylinidae	7,407	37.1	62	28.6
2. Silphidae	4,300	21.5	7	3.2
3. Nitidulidae	3,575	17.9	24	11.1
4. Hydrophilidae	1,427	7.1	— ^a	—
5. Leptodiridae	979	4.9	6	2.8
6. Histeridae	684	3.4	17	7.8
7. Carabidae	463	2.3	23	10.6
8. Ptiliidae	390	2.0	4	1.8
9. Scarabaeidae	385	1.9	17	7.8
10. Scolytidae	266	1.3	6	2.8
Minor Families (5)	73	0.4	16	7.4
Adventitious families (18)	43	0.2	35	16.1
Totals	19,992	100.0	217	100.0

^a All hydrophilids were in the genus *Cercyon*, but current taxonomic literature could not identify specimens to species.

Curating.—The field-collected beetles were curated in the Entomological Laboratories of Fordham University, Bronx, New York 10458. Each of the approximately 20,000 adult beetles was individually pinned, labeled, and then stored in 40 of Fordham's "California Academy of Sciences" style insect drawers.

Results and Discussion

Necrophilous and carpophilous families.—Almost 20,000 beetles were collected during the 8-month period (April thru November) from 6 traps baited with fish and 6 with melon. Six traps (3 pairs with each type of bait) were located on the dry slope and the other 6 in the wet valley. The trapped Coleoptera were concentrated in 10 major families (19,876 beetles or 99.4% of total) as shown in Table 1. In addition, there were also 5 minor families which included only 73 individuals or 0.4% of the total and were associated with fungi or decaying organic material. Finally, 18 other families (43 beetles or 0.2%) were categorized as "adventitious," i.e., phytophagous forms or wanderers on the forest floor which were probably accidentally caught in the traps. From the point of view of numbers of species, 217 species were collected and identified. Of these, 76.5% belonged to the 10 major families, 7.4% to the 5 minor families, and 16.1% to the adventitious families.

10 major families.—Considering that almost 20,000 individual Coleoptera were collected in the combination fish-melon and slope-valley traps, there

Table 2. Seasonal summary over an 8-month period of the 10 major families of Coleoptera collected from traps baited with fish for necrophilous beetles and melon for carpophilous species in a dry slope habitat and an adjacent wet valley.

Month	Slope			Valley			Total		Monthly	
	Fish	Melon	Total	Fish	Melon	Total	Fish	Melon	Total	%
Apr	227	114	341	337	95	432	564	209	773	3.9
May	978	247	1,225	547	255	802	1,525	502	2,027	10.2
Jun	509	765	1,274	356	639	995	865	1,404	2,269	11.4
Jul	1,309	574	1,883	1,371	747	2,118	2,680	1,321	4,001	20.2
Aug	793	1,536	2,329	975	1,148	2,123	1,768	2,684	4,452	22.4
Sep	960	858	1,818	791	914	1,705	1,751	1,772	3,523	17.7
Oct	260	672	932	217	1,018	1,235	477	1,690	2,167	10.9
Nov	159	172	331	138	195	333	297	367	664	3.3
Totals	5,195	4,938	10,133	4,732	5,011	9,743	9,927	9,949	19,876	100.0
Percent	51.3	48.7	51.0	48.6	51.4	49.0	49.9	50.1	100.0	

were some interesting, if not surprising, similarities in the overall totals (Table 2). For instance, 9,927 necrophilous beetles were collected in the fish traps, and almost an equal number (9,949) of carpophilous beetles were on melon. Similarly, the slope traps (fish-melon) accounted for 10,133 beetles, and the valley bait (also fish-melon) trapped 9,743. There are no significant statistical differences between these pairs of numbers. However, when the families and especially the species are examined more closely, then differences are seen in the preferences for the bait (fish or melon), and to a lesser degree for the habitat (slope or valley). A more complete picture of this *Part 1* overview will be given in subsequent papers which will analyze in detail the trophic and geographic differences not only between the 10 major families, but also among the species of each.

For the purpose of this introductory presentation, however, a brief summary of the 3 most numerous families (Staphylinidae, Silphidae, Nitidulidae) will be given below (Table 3). These 3 families comprised 76.5% of the individual beetles collected in this study, and 42.9% of the total species.

1) *Staphylinidae*.—The staphylinids contained more individuals (7,407 or 37.1%) and more species (62 or 28.6%) than any other family. They were attracted to melon over fish by a 2:1 ratio (4,704:2,703), and there was a 10% difference between the number in the valley (4,103 or 55.4%) and the slope (3,304 or 44.6%).

2) *Silphidae*.—Although this family ranked 2nd in the number of specimens (4,300 or 21.5%), it dropped significantly to 6th place in the number of species, having only 7 species represented or 3.2% of the total. In addition, unlike the Staphylinidae, these beetles were almost absent from the melon traps (only 0.8%). The slope also reflected a similar reversal in niche

Table 3. Comparison of the 3 most numerous Families of Coleoptera (Staphylinidae, Silphidae, Nitidulidae) collected from traps baited with fish for necrophilous beetles and melon for carpophilous species in a dry slope habitat and an adjacent wet valley over an 8-month period (April thru November).

Family		Slope			Valley			Total		
		Fish	Melon	Total	Fish	Melon	Total	Fish	Melon	Total
Staphylinidae	No.	1,171	2,133	3,304	1,532	2,571	4,103	2,703	4,704	7,407
	%	35.4	64.6	44.6	37.3	62.7	55.4	36.5	63.5	100.0
Silphidae	No.	2,457	24	2,481	1,807	12	1,819	4,264	36	4,300
	%	99.0	0.1	57.7	99.3	0.7	42.3	99.2	0.8	100.0
Nitidulidae	No.	262	1,888	2,150	144	1,281	1,425	406	3,169	3,575
	%	12.2	87.8	60.1	10.1	89.9	39.9	11.4	88.6	100.0
Totals	No.	3,890	4,045	7,935	3,483	3,864	7,347	7,373	7,909	15,282
	%	49.0	51.0	51.9	47.4	52.6	48.1	48.2	51.8	100.0

preference, accounting for 57.7% of the trapped silphids, while only 42.3% were collected in the valley traps.

3) *Nitidulidae*.—This was the 3rd most common family with 3,575 or 17.9% of the total individuals. Because of the few number of silphid species noted above, however, the Nitidulidae moved up to become the 2nd largest family as to number of species (24 or 11.1%). Of these, strong preferences were shown for melon (88.6%), while 60.1% were trapped on the slope. Hence, the nitidulids seemed to combine the preference of the Staphylinidae for melon with that of the Silphidae for the slope. Another way of looking at these data would be that the Nitidulidae occupied niches which were less competitive when considered in relation to the other two families.

Phenology.—During the 8-month period of this study (Table 2), only 773 beetles (3.9%) were collected in April. This increased to 2,027 (10.2%) during May, and 2,269 (11.4%) in June, so that both months were quite similar. However, the peak months were July (4,001 or 20.2%), August (4,452 or 22.4%) and September (3,523 or 17.7%). The October collecting (2,167 or 10.9%) was similar to that of May and June, while November (664 or 3.3%) returned to the low of April. This can be summarized by saying that 60.3% of the beetles were trapped during the peak months of July, August and September. But only about half as many (32.5%) were collected in May, June and October. As a result, April and November being the beginning and the end of the season, accounted for only 7.2% together.

In reference to the 3 most numerous families, the Staphylinidae peaked from August through October. On the other hand, May, July and August were the months in which the Silphidae were best represented, while the Nitidulidae were trapped most frequently in June, August and September.

These data indicate that August was the high month for collecting all 3 families. This was apparently due to phenological overlap, although the other months show some temporal niche-splitting.

Many species of beetles were represented by a very small 1st generation early in the spring or summer. After this initial appearance, they were not trapped again for a long period during the remainder of the summer, but reappeared with a large 2nd generation in the fall. Species with such a pattern are usually designated as bivoltine, but it should be pointed out that many spring specimens may have been overwintering adults (especially among the Carabidae). In this case, such species are actually univoltine. Winter diapause and summer aestivation are factors which should be studied in this regard. Hence, the continuing need in insect ecology for observation on the bionomics of each species in the field.

The results show that certain species are attracted to decomposing fish (necrophilous) and others to melon (carpophilous). However, in both cases, many of the beetles are actually predatory, and some are general scavengers. Closely related species are usually separated temporally, most often by fortnightly periods. Some of the seemingly weaker species emerge earlier than the stronger ones, and so gain a definite competitive advantage in time.

Fuller (1934), working for 4½ years in Australia, recorded far fewer species of beetles on carrion than is reported in this study, although the families represented were remarkably similar. Howden (1950) recorded 98 species of Coleoptera on carrion. The Families Staphylinidae, Histeridae and Carabidae made up 50% of the beetles. She concluded that the effect of the surrounding flora on a carcass was expressed in moisture relationships, and our data on the dry slope and wet valley differences support this interpretation. She found that more beetle species and individuals participated in the succession in the spring than in the summer. In autumn, the carrion regained some of the lively and abundant qualities of the spring, but the fauna was not as rich.

Walker (1957) also showed that the succession of organisms associated with decaying material is influenced by variation in vegetation and microclimate. In addition, in an area of only a few hectares, the animals associated with similar decaying materials in adjacent habitats may be quite different. He used cantaloupe, fish and cornmeal as bait. The major groups of the trapped beetles included 15 species of staphylinids, 7 nitidulids and scarabs each, 3 histerids, 2 carabids, and 1 species each of hydrophilid, leioidid, ptiliid, mycetophagid—all taken on cantaloupe. In the fish baited traps, the following families of Coleoptera were recorded: 18 species of staphylinids, 8 species each of silphids and histerids, 6 scarabs, 2 hydrophilids and trogids, plus 1 nitidulid, carabid, dermestid, ptiliid, monotomid. Walker correctly noted that most of the field research on how attractive a bait is at certain times in its decay cycle fails to take into account whether the species

are naturally available as adults at the time of the study. Our work at Fordham attempts to elucidate this neglected aspect of insect ecology.

Reed (1958) reported an analysis of dog-carcass microcommunities with particular reference to seral development, seasonal variation and environmental factors. He found that the summer months had peak populations with 217 species of insects of which only 96 were coleopteran species.

Payne (1965) used as carrion baby pigs (*Sus scrofa* L.). Carrion free of insects decomposed very slowly, merely drying and retaining its form for many months. However, 90% of the carrion open to insects was removed in 6 days. Only 2 coleopterous families, the Staphylinidae and Histeridae, were reported during the 2–3 weeks of his study. He determined that by the 5th day of exposure of pig carrion, beetles were the dominant adult insects present. Payne found that the activities of insects were more influenced by temperature than by any other environmental factor, while moisture ranked second. Payne agrees with Fuller (1934) in stating that insects hasten carrion disintegration by dissemination of bacteria, secretion of digestive juices, and by the mechanical processes of burrowing and tunneling through the carcasses. The Coleoptera and Diptera comprised 60% of the total fauna taken on carrion. Of 522 organisms collected, 422 species were insects, with 217 being beetles. Once again, the staphylinids and histerids were the dominant Coleoptera (92 species or 42.4%).

Extensive field studies on carrion beetle responses to poikilothermic (fish) and homiothermic (chicken) bait have been done by Shubeck (1968, 1969, 1971, 1975a,b, 1976a,b) over many years using specially designed pitfall traps as well as specially designed ground and air traps. As in our study, he agreed with Walker (1957) that the differences in the species collected were due to the degree of carrion decay within the habitats, which in turn were caused by differences in microclimate. At the Family level, the overwhelming majority of beetles taken were Silphidae, Staphylinidae, Histeridae, Leiodidae, Scarabaeidae and Nitidulidae. Similar supporting studies have been done using lizards and toads (Cornaby 1974), and mammals (Johnson 1975).

The data obtained in our own field collections at the Fordham Ecology Center also fit very well with the population generalizations of Preston (1948). He noted that in any association there are just as many very rare species as there are common ones, but species of moderate abundance are vastly more numerous than either. Wilhm (1968) stated that the widespread similarity in numerical distribution patterns of individuals and species is one of the most interesting and still unexplained properties of ecological systems. Our results concur with these conclusions that a relatively small percentage of the species contain a large number of individuals, and a large percentage contain only a small number of individuals. Hence, the necrophili-

lous and carophilous Coleoptera can be used as ecological indicators of the numerical and temporal relations between species.

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Department of Biological Sciences, Fordham University, Bronx, New York 10458.

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PLATANThERA CRISTATA (MICHX.) LINDL., A NEW HOST FOR
THE RED-BANDED LEAF ROLLER¹

T. L. McCabe and C. J. Sheviak

Abstract.—Larvae of the tortricid, *Argyrotaenia velutinana* Wlk., have been recorded feeding on the seeds of the orchid, *Platanthera cristata* (Michx.) Lindl., on Long Island, New York.

Four plants of the orchid, *Platanthera cristata* (Michx.) Lindl., were collected August 15, 1979 from pitch pine barrens on Long Island, New York, and were subsequently cultivated at Albany. Within ten days two plants showed webbing and frass resulting from the activity of a caterpillar in each inflorescence. By October 28th, a mature larva of the red-banded leaf roller, *Argyrotaenia velutinana* Wlk., was found feeding within a seed capsule. Normal larval behavior is leaf rolling, i.e., it feeds and rests from within a curled leaf (Forbes 1923).

Chapman and Lienk (1971) gave host records for a great many deciduous and coniferous trees. They stated that the moth is of low incidence in nature making it difficult to identify native primary hosts and that virtually all reports of secondary hosts have been from the immediate vicinity of apple orchards, where it is a major pest. The present collection was made in an undisturbed community. The orchid is a coastal plain species that reaches its northern limits on Long Island. The moth is found throughout the East.

The larvae were first noticed toward the end of the orchid's period of bloom, indicating that the eggs were laid in the mature inflorescence at about the peak of flowering. This suggests that the moths were attracted to the flowers. The moth proboscis is less than two millimeters long, and, as the orchid's nectariferous spur is about five millimeters long, the moth probably does not serve as a pollinator. The larvae constructed a loose silken tube running nearly the length of the inflorescence, and ate the contents of six or seven seed capsules, entering each at the middle, before pupating. One larva pupated within a seed capsule on 8 October and was refrigerated on 28 November. The pupa was reintroduced to room temperature on 16 February and a male emerged on 2 March 1980. The pupal exuvia protruded from the capsule.

Pupal exuvia, mature larval head capsule, reared adult, and specimens of

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the orchid are coded tlm 79-78 and CJS 1606, respectively, and are deposited in the New York State Museum.

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New York State Museum, State Education Department, Cultural Education Center 3132, Albany, New York 12230.

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EVOLUTIONARY ORIGIN OF BEES
(HYMENOPTERA: APOIDEA)

U. N. Lanham

Abstract.—Bees are generally supposed to be descendants of sphecids wasps, largely on the basis of similarities in thoracic structure. If it be assumed that these similarities are convergent, resulting from independent evolution for high-precision flight, then an argument can be made for a close relationship between bees, ants, and scolioid wasps.

In 1951 I wrote that "the pollen and nectar-feeding bees arose from the primarily predaceous wasps . . .," even then a well-worn phrase, and went on to say that ". . . but acceptable theories as to the transition between the two modes of life have not been worked out." This last also was true then and is now, in spite of the publication of a book on the evolution of the Hymenoptera (Malyshev, 1968). Nor does the present paper remedy the situation, in the sense that "at last the mystery is solved." Nevertheless aculeate phylogeny, although an inherently frustrating subject, in the manner of all phylogenetic studies, is worthwhile insofar as it organizes observation of the immense complexity of morphology and behavior to be found in the aculeate Hymenoptera.

It is the modern consensus that the group of wasps that gave rise to the bees is the sphecids. Two recent works supporting this theory are those of Bohart and Menke (1976:31) and Brothers (1975). Among the sphecids, Malyshev (279ff) selects the pemphredonines as the group offering a transition from sphecid to bee. Some of these are small wasps nesting in twig cavities that they fill with small, soft-bodied insects such as aphids. Individual cells along the length of the twig cavity are lined with a tough transparent membrane produced by mandibular glands of the female. The most wasp-like of the bees, according to Malyshev, are the hylaeines, some of which also nest in twig cavities with individual cells lined by thin transparent membranes. Aphid-feeding pemphredonines, Malyshev reasons, could have shifted from aphids, themselves a mixture of protein and honeydew, to a pollen-nectar food store for the young. This would mark the genesis of bees.

Hylaeine bees and pemphredonine wasps resemble each other both superficially and in those characteristics, mainly involving the thorax, which in Brothers' opinion tie all of the bees closely to the sphecids. A discussion of these common characters will be deferred for the moment to concentrate on the differences. If a *Hylaeus* is examined carefully at high magnification, it will be found that at least a few of the hairs are compound (branched or

feathery). Such hairs are especially abundant in the short filter fringe on the prothoracic lobe, which covers a large spiracle. Hylaeine bees are somewhat atypical in being relatively hairless; most bees are abundantly long-hairy, with many branched hairs. In fact, the presence of branched hairs is absolutely diagnostic in comparing bees with sphecids: none of the sphecids have such hairs; all bees do have them.

It is unreasonable, in my opinion, to think that the few compound hairs of the hylaeines represent a basis for the selective evolution of compound hairs in the bees. Rather, they represent the situation found in the many species of parasitic bees which do not have to transport pollen in external baskets or brushes; these are also nearly hairless, and also have a few compound hairs. Hylaeines transport pollen to the brood cells in the crop, gathering the pollen with their front legs into the mouth. It seems more reasonable to think that they display a specialized reduction of hairs such as occurs in the parasitic bees, made possible by the crop-transporting mode. Better representatives than the hylaeines of primitive bees are perhaps the euryglossines, limited to Australia, which are not superficially wasp-like. Although these, like hylaeines carry pollen in the crop (presumably the primitive mode) rather than externally, they are abundantly long-hairy, with many compound hairs. The hylaeines could then be regarded as specialized descendants of the euryglossines.

It is difficult to imagine that the presence of a few compound hairs in the manner of the hylaeines would provide the broad and stable base necessary for the evolution of compound hairs which, judging from their absolute absence in the many thousand species of sphecid, vespids, pompilids, tiphiids, and scoliid wasps, are not evolved except in highly unusual circumstances (Lanham 1979). If we take the compound hairs as representing a fundamental rather than trivial character of the bees, then we are led to consider the possibility that the pemphredonine-hylaeine transition is not the best hypothesis for the evolutionary origin of bees.

Another difference that leads to the same conclusion is one which for some reason escaped general notice until rather recently (Lanham 1960 and Bohart and Menke 1976:27). This is the presence on the hind leg of the sphecid of a strigil composed of a hind tibial spur (sometimes modified) facing a brush-lined concavity at the proximal end of the basitarsis. When the wasp disposes of particulate debris, it pulls the opposite hind leg, which is stocked with the particles by a variety of grooming movements, through the strigil in the manner that the antenna moves through the strigil of the front leg. In all bees the hind strigil is absent, and debris is disposed of by shuffling together the two brushes on the inner surfaces of the widened hind basitarsi. It has been suggested that the evolution of the basitibial brush in the bees obliterated the ancestral sphecid strigil, but it seems to me that the brush is a character which has been inherited directly from primitive astrig-

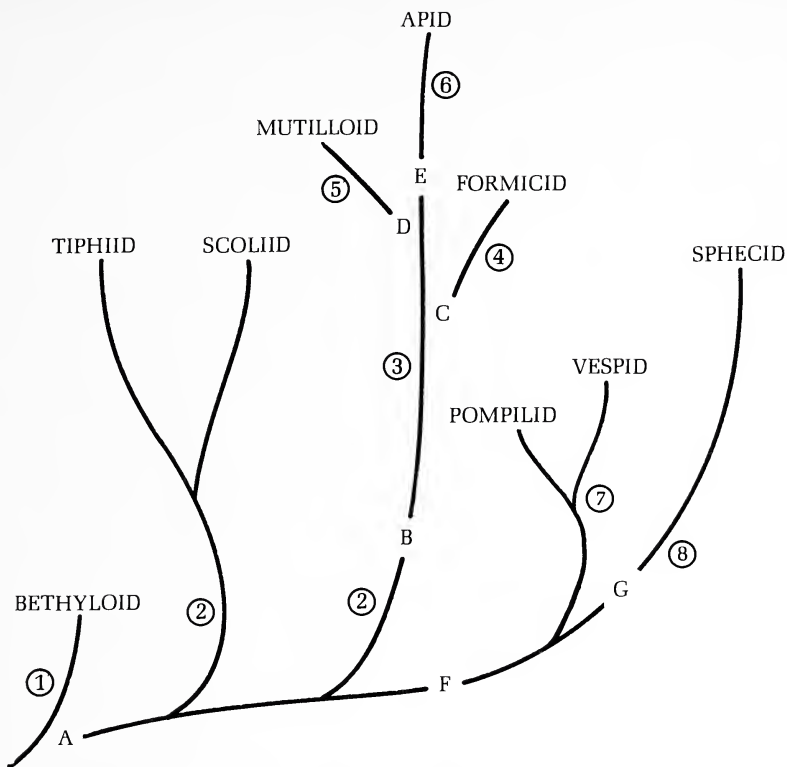


Fig. 1. Phylogenetic tree of the aculeate Hymenoptera. Letters refer to strategies or major adaptive shifts, numbers to the one or more major taxa that result.

ilate aculeates without the intervention of a strigilate phase. One sees on the slender basitarsis of some primitive ants the apically directed hairs which make of it a rather bee-like, one-way disposal apparatus when shuffled against the opposing brush. Wilson (1962:413) has described this cleaning movement in certain primitive ants, and I have observed it in the non-aculeate *Pelecinus*.

If the compound hairs and absence of the hind strigil are taken so seriously that it is thought best to shift the origin of bees to an area of the aculeates where both characters are present, then the only site available in the living fauna is one near the ants. Ants are so specialized that they could not serve as ancestors for the bees, but both could be considered to be derived from a stock of astrigilate wasps with compound hairs at some stage in the life cycle. In addition, as will be brought out subsequently, the ancestral stock of the bees and ants would be social and nest in cavities, most likely in wood.

It is obvious that if the origin of bees is shifted away from the sphecids,

then the similarity in thoracic structure must be regarded as the result of convergent evolution. Brothers, who has made a detailed study of the aculeate thorax in his phylogenetic studies, finds three characters of the thorax which in his numerical procedure tip the balance heavily in favor of a close bee-sphecid relationship.

1. The antero-lateral corner of the mesoscutum is enlarged so that it extends far anterior to the tegula. This is Brothers' character state 21.2, which "arose uniquely on internode 4-5 and thus is a very good indicator of the holophyly of the sphecid and apid groups." The position adopted here is that it arose on two occasions, once within the strigilate wasps, once within the astrigilate wasps.
2. The ventral angles of the propodeum are slender and so elongate that they almost or quite encircle the thorax, meeting (or nearly so) at the ventral midline. This is character state 23.2, which "is uniquely present in the sphecid and apid groups and apparently arose on internode 4-5, thus forming a strong indicator of the holophyly of this grouping." The position taken is that this structure is the inevitable consequence of the enlargement of the antero-lateral corners of the mesoscutum. There is no other way in which a broad support to brace the prothorax (which carries the industrially important front legs) against the mesothorax can be managed, when the slanting abutment against the anteriorly narrowed mesoscutum of other aculeates is abolished. Thus character state 23.2 is a mechanical correlate of 21.2 and cannot be weighted as a separate evolutionary event.
3. The origin of the postphragmal muscle shifts posteriorly to a position on the dorsal surface of the apparent propodeum. Brothers interprets the origin of this muscle as always being the metapostnotum, so that the large "triangle" of the propodeum is the metapostnotum. This is character state 35.3, which he says is "unique in the Aculeata and apparently in the Hymenoptera as a whole. This remarkable modification of the metapostnotum which is present in the sphecid and apid groups provides extremely strong evidence of the holophyletic association of these groups, having arisen on internode 4-5." The small postphragmal muscle inserts on the posterior surface of the 2nd phragma, a curved sclerotized band whose anterior face provides the area for the origin of the longitudinal indirect flight muscles. In character state 35.3 the phragma becomes vertical instead of slanting far back of and below the insertion of the postphragmal muscle (Brothers 1976, figs. 1-12). When the phragma became vertical, the bundles of the longitudinal muscles become more nearly equal in length, and the functional center of the phragma has retreated, making necessary a posterior shift in the origin of the postphragmal muscle. I am unable to explain the functional significance of

this, except to say that it would seem reasonable that equal-length longitudinal fibers would deliver more smoothly the power that arches the mesoscutum and depresses the wings. At any rate, the net result of all three character states is the consolidation of the indirect flight muscles (which furnish nearly all of the energy of flight) into a compact subspherical or elliptical mass. It may be that character state 35.3 is also part of the only solution to the problem of enhancing flight ability (a matter to be discussed in the next section) and thus, like state 23.2, not to be weighted as independent of the other two character states.

Enlargement of the antero-lateral corners of the mesoscutum is here taken to be the basic morphological character from which other major thoracic characters follow. Its primary function is that of increasing the area of insertion, hence the size of the vertical (elevator) indirect flight muscles. Judging from the figures of the thoracic musculature of *Apis* in Snodgrass (1942) the longitudinal and vertical muscles are of equivalent size. This would mean that the upstroke would deliver approximately the same power as the downstroke. This aspect of the functional morphology of the aculeate thorax is a complex subject that has not been investigated. However, nearly every field entomologist has seen the extreme example: the large anthophorine bees or the bembecine wasps, which hover perfectly still, then accelerate swiftly to a speed where they become invisible (an object this size becomes invisible at about 35 miles per hour) and with such accuracy that they easily avoid the net. No other aculeates approach the powerful and high-precision flight of such bees and sphecids. Intuitively it would seem that continuous delivery of power at a uniform level would give an aerodynamic fine-tuning not attainable in the presumably more ragged flight of a wasp with a considerable difference in delivery of power in upstroke and downstroke. The effect on flight musculature of the anteriorly narrowed mesoscutum (characteristic of all aculeates above the bethyloid level except sphecids and bees) can be seen in the figures by Duncan (1939) of the thoracic musculature of the vespid wasp *Vespula pennsylvanica* (Sauss.). Here the longitudinal indirect flight muscles are, says Duncan, enormous, being much the largest muscles of the body. The size of the vertical muscles, which insert laterally on the mesoscutum, is limited by the shortened area for insertion as compared with the longitudinals. Some tiphiid and pompilid wasps seem to have the anterior portion of the mesoscutum squared off rather than narrowed, but this is illusory. If the long, overlapping pronotal collar is pried off, underneath can be seen the sclerotized, narrowed end of the mesoscutum.

In brief, it is proposed that a major adaptive characteristic was arrived at independently in the bees and sphecids. This adaption is the high-precision flight made possible by the enlargement of the elevator flight muscles. In

the bees, this is useful in flower visiting and return and entry to a nest. In the sphecids wasps it is useful in visiting flowers for fuel, searching for and catching prey, and returning to and entering a nest. In both it is, especially in the spacious, competitive desert environment, helpful in eluding birds or such swift insect predators as asilid flies or, indeed, some of the sphecids wasps themselves.

With the bees now in theory detached from the sphecids, a possible home for them is provided in the accompanying phylogenetic tree. Letters indicate major strategies or adaptive advances that separate the tree into a number of sectors, each of which contains one or more higher taxa.

Bethyloids (sector 1) are for the most part small to minute parasitic wasps. These probably could not be directly ancestral to any of the aculeate groups with large-sized individuals, since wing venation is much reduced in the forewings and absent in the hindwings. The genus *Scleroderma* of the bethylids has long figured in speculations on the origin of ants (see Malyshev p. 217ff). A female lays many eggs on a large host larva and stays with it, providing rudimentary care for the young. Eventually a few generations of wasps are present on a single larva, forming a pre-social aggregation including many wingless, ant-like females. The phylogenetic position of the bethyloids is not well understood, but they have a mixture of characters belonging to other superfamilies, so could possibly be specialized descendants from a primitive stock of aculeates.

Strategy A is a modification of the parasitic mode in which relatively large and powerful wasps dig through loose soil or rotting wood in a more predatory fashion after beetle larvae which they paralyze with the sting, and on which they lay a single egg. Primitively they leave the prey in place, but some dig a cell which shelters the larva and the subsequent wasp larva, or even move the host larva to another shelter. Sector 2 includes two major families, the scoliids and tiphiids, which are particularly abundant in the warmer parts of the world and with many species in the Southern Hemisphere. These families, and two or more smaller families, are sometimes put in a superfamily, the Scolioidea. They can be termed the non-nesting astrigilate wasps, although as already pointed out, the behavior of some of the species grades into the better defined nesting behavior of the more advanced wasps.

Strategy B is an adaptive shift in which some of the astrigilate wasps use arboreal nesting sites where they store prey in cavities in wood. These clean and dry sites in the tropical forest might have proved a major new nesting environment which made possible a train of events leading to the ants and bees. These nesting cavities, which would be enlarged, using the mandibles, were from the beginning, and remained so during the early stages of bee evolution, communal nest chambers. This communal mode leads easily into progressive feeding, then through pre-social communities to true societies. One of the consequences of moderately large societies, it seems to me, must

have been the opportunity to widen the food base. Primitive hunting wasps, for example, might be transformed from fairly specialized hunters into general hunters and scavengers, bringing all kinds of edibles into the nest. In some instances, the at first tentative use of a new food source might open up an area for specialization. While most modern ants, for example, are generalists, a few are specialists on such prey as other ant species or terrestrial isopods. Social aculeates living in communal nests produce a significant evolutionary event—larvae with long hairs (Lanham 1979). Long-haired larvae, otherwise unknown in the aculeates, occur in about 90% of the genera of ants and in many of the genera of allodapine bees. Furthermore, at least one species of allodapines and about half the genera of ants have compound larval hairs. The modified hairs of ant larvae have a greater variety of form than any other feature of ant morphology. Some 30 types have been described and appear to be adaptations for various characteristics of life in communal cells (Wheeler and Wheeler 1976). Communal nests (with only a handful of apparently irrelevant exceptions) are known among the aculeates only in the ants (essentially all) and in some bees (some allodapines and *Bombus*). Thus, the bees have been placed in a phylogenetic milieu that could explain the two features separating them from the sphecids: absence of the hind strigil and presence of compound hairs.

Nowhere have there been found scolioid wasps that suggest the kind of transition made in strategy B. There is only one extensive, unexplored group remaining among the larger scolioid wasps. This is the subfamily Thynninae, with about 500 species in Australia and some hundreds in South America. All the known species have winged males and wingless females. Males are larger than the females and carry them about during mating. For most species, the females are observed only when found on the conspicuous, flower-visiting males. Some spend most of their time burrowing about in the ground in search of beetle larvae. Probably the biology of fewer than 5% of the species is known in Australia (Burrell 1935). The females of these sting the host larva, oviposit, and leave it in place. In only one species, which is taxonomically isolated from the rest of the thynnines (*Diamma bicolor* Westwood) is the female known to drag its prey to its own burrow. In species other than *Diamma* the males, unlike nearly all other aculeates, play a role in the economy of the wasp other than fertilizing eggs. Some carry the females, attached to the tip of the male abdomen, to feeding sites, either flowers or honeydew-secreting scale insects, where they position themselves so that the female can drink. Others carry nectar or honeydew to the female, carrying a droplet in a basket of hairs on the underside of the head (Given 1954), or feeding by regurgitation. Perhaps somewhere in this ancient and abundant group there may be found small societies of females (even attended by solicitous males) which would bear witness to the former existence of sector 3. A few species live in wood.

This is the place to point out that the delineation of a clean, arboreal

communal nesting site as the site for the evolution of the ancestral stock of bees may have fashioned a two-edged sword, which may provide evidence that it was indeed the sphecids wasps that gave rise to the bees. It has been rather recently discovered (see Matthews 1968 and Bohart & Menke 1976:172) that a genus (*Microstigmus*) of small neotropical pemphredonine wasps live in diminutive (18×12 mm) bag-like nests suspended from the underside of the leaves of forest trees. The species *M. comes* Krombein, measuring about 3 mm in length, constructs the nest from fibers scraped from the undersurface of the leaf. It would seem that this cavity would offer the ideal opportunity for the establishment of a communal nest, yet this species remains determinedly sphecid, constructing in the loose fibers filling the lower half of the bag up to 15 separate cells, with one naked larva reared in each. Nevertheless, one can imagine that in the yet unstudied species of the genus there may be found an evolutionary sequence in which cell making is abandoned and the larvae have become hairy, in the manner of other aculeates living communally. Only 17 species of *Microstigmus* are listed in the Bohart and Menke catalogue, but apparently more than a hundred more have since been discovered. These wasps represent a most interesting departure from the biologies of other sphecids, but it is probably a specialization too recent to have been involved in the evolution of the bees or ants or both.

Strategy C was the commitment to on-foot foraging by a wingless female worker caste. Reproductive males and females are generally winged, but flight ability is degenerate, serving to form mating swarms and to aid in dispersal. This social, on-foot foraging mode of existence laid the foundation for the evolution of the most successful group of aculeates, the ants, with a number of species exceeded only by the bees and in numbers exceeding all other aculeates. Although they are dominant in the arboreal fauna of the tropics below 2,500 meters of altitude, the key to their success has been the invasion of the nutrient rich ground-air interface, where they rule in all the sunwarmed land environments on the earth.

Sector 4 is the living family Formicidae, the ants. In the clean arboreal environment there was no selection of the hind strigil and the ants remained almost entirely astrigilate. A few of the ground-dwelling genera, such as *Neoponera*, have a fairly well developed hind strigil, but these occur in only few and scattered instances, and are taken to be independent origins of this structure. The other thousands of species of ground dwelling astrigilate ants are able to take care of hygiene by mutual grooming and the fact that the legs are so long that the hind legs can be pulled through the strigil of the front legs.

As has been said, probably about half the genera of ants have larvae with compound hairs. A few species also have compound hairs in the adult stage. Two are known in North America. *Triglyphothrix striatidens* (Emery), an

introduced species, has trifold hairs. The larva has hairs with "multifid tips" (Wheeler & Wheeler 1973). The native species *Acanthomyops plumipilosus* (Buren) has plumose hairs, the genus itself generally has denticulate hairs as larvae. The similarity between larval and adult hairs, particularly in the peculiar first example, tends to support my contention (1979) that the genetic expression of compound hairs can be shifted from the larval to the adult stage. However, the numerous examples of exotic ants with odd shaped hairs in the adult need to be checked against larval morphology to learn more of this phenomenon.

Strategy D is a rather minor development in which the females usually become wingless and solitary parasites of the nests of other Hymenoptera. Some extra-North American species are said to parasitize larvae of other insect orders.

Sector 5. The great majority of species are in the family Mutillidae. The families Eotillidae, Typhoctidae, and Anthoboscidae (females winged) are included in this sector because at least some of the species of each have compound hairs, thought to be sporadic, genetically based reminiscences of a cavity-nesting past.

Strategy E is the specialization for pollen feeding that marked the origin of bees. One other group of aculeates, the masarine vespids, also provides its young with a food store of pollen, but this was a relatively small scale venture, involving less than a thousand species. Bees total about 20,000 species, and have more than any other group cooperated in the evolution of the flowering plants. As said in the discussion of Sector 3, the social mode makes possible a widening of the nutritional base. Among the edibles brought in to these early societies there would certainly be pollen, which was available in the Cretaceous, when these early phases in hymenopteran evolution were taking place (Evans 1973). Instances in which pollen becomes an important food source would produce overwhelming selective advantage for the changes in control genes that would transfer expression of compound hairs to the adult stage. The pollen-gathering masarine wasps, mentioned above, did not have a communal-nesting ancestry, never had compound hairs in their evolutionary background and the modern species do not have compound hairs.

Sector 6 comprises the bees, usually put in a superfamily divided into several families. Thus use of the term "apids" here is merely a convenience, following the terminology used by Brothers, and does not represent a statement as to the rank given the taxon. It is supposed here that the bees were primitively social arboreal cavity nesters. Today only a minority of bees are social, either primarily or secondarily, being represented by several hundreds of species, most of them dwelling in arboreal nests constructed of wax and resins, but the allodapines resembling at least superficially the supposedly primitive mode in which there are small communal nests in twig

cavities. Among the wax-nesting bees are the usually nonarboreal *Bombus*, of which a few species nest communally during at least part of the seasonal cycle. None of these have long-hairy larvae. In the more primitive bee societies, reversion of social bees to the solitary mode, or even the reverse, is quite feasible (Wilson 1971:102). The vast majority of living bees are solitary, are especially well represented in arid regions, and usually nest in the ground in the manner of many sphecids species, providing each larva with its own earthen cell.

Strategy F represents the transition between the primitive astrigilate non-nesters to the strigilate ground nesters. Here the burrow and the cells are carefully constructed, with a brood cell of compacted earth. The nest is often multicellular, thus being visited often between foraging trips, and even when unicellular, with several burrows being dug, the cell is often provided with several prey insects or spiders. It is here postulated that the development of the hind strigil is of adaptive value in keeping clean in this mode of life, and in helping maintain hygiene in the brood cells.

Sector 7 includes the pompilids (spider wasps) and vespid wasps. Pompilids are either ground nesters (sometimes using a preformed cavity) or construct above-ground nests of mud cells. All are solitary. They are rather poor fliers, and have a tendency to collide with rather than gracefully alight upon flowers. They tend to do much of their hunting on foot. The primitive subfamilies of the vespids are solitary, constructing their cells in the ground, or in twigs building mud cells above ground. The advanced vespine wasps build arboreal nests of papery materials (sometimes the same sorts of nests are made in large underground cavities). These wasps are always social. Each larva has a separate paper cell.

Strategy G involves the evolution of high-precision flight, the morphological expression being the expansion of the antero-lateral corners of the mesoscutum. It may be that the failure of this character to develop in the vespids was due to the evolution of the yet unexplained peculiarity of the wings, which in all but a few primitive forms are kept folded lengthwise when not in use. This might have some advantage in the nest life, but might well be a liability in flight. Its advantage in the sphecids is probably a reflection of their generally more intense foraging and nesting activity: the frequent visits to flowers for nectar for fuel, alternating flight and on-foot pursuit of prey, sometimes the prey captured in flight, and the wasp hovering alertly, ready to dash away at any disturbance.

Sector 8 includes the sphecids wasps. The biology of the exceptional social forms was discussed earlier. The thousands of species of solitary forms, mostly ground nesting, prey on insects or, more rarely spiders. Unlike the bees and scoliids, there are few endemic or aberrant groups in Australia.

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University of Colorado Museum, Box 218, Boulder, Colorado 80309.

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TRANSMISSION OF VIBRATIONS ALONG PLANT STEMS:
IMPLICATIONS FOR INSECT COMMUNICATION

Paul D. Bell

Abstract.—Many insects are known to communicate with percussive vibration and vibrations transduced with acoustic songs via plant tissue. Artificial percussive vibrations degrade in acceleration and velocity away from a vibration source along plant stems; the free end distorting and losing energy faster than the fixed end. Woody stemmed plants vibrate within a narrow frequency band and thus transmit signals further than fleshy ones.

Nutritional imperatives, oviposition sites and predator avoidance constitute the major reasons many insects frequent certain species of plants. Nevertheless, another use of plants to insects may be to act as a communication channel. Representatives from many insect orders vibrate their plant substrate during mating and aggressive behavior (Table 1).

It is well documented that insects detect substrate vibrations with sensory neurons innervating the tympana and subgenual organs (Cokl et al. 1977; Fudalewicz-Niemezyk et al. 1978; Huber 1978; Kalming et al. 1978).

Here are investigated the vibration transmission characteristics of various plants that tree crickets, *Oecanthus* spp. (Orthoptera: Gryllidae), are found on north of Huttonville, Ontario, Canada. The acceleration, velocity, wave form and duration of induced artificial vibrations that approximated *O. nigricornis* (Walker) percussive vibratory signals were measured from plants that tree crickets do and do not mate on. The transmission characteristics and vibrational physics of these plants below (fixed end) and above (free end) a vibrational source were determined.

Materials and Methods

An Exact 126 signal generator was set to deliver a 5 ms, 100 Hz sinusoidal pulse every 5 sec. A Marsland woofer converted these pulses into vibrations via a plastic probe. These signals as modified by the plant were measured with a Bruel and Kjaer 4344 accelerometer and a B.&K. 2304 impulse precision sound level meter for acceleration and velocity. The accelerometer and probe were mounted to the plant with a thin layer of bees' wax as outlined by Brock (1972). The vibrations were recorded with a Uher 4000 Report IC tape recorder and displayed on a Tektronix 455 oscilloscope (Fig. 1).

Ten each of orchard grass (*Dactylis glomerata* L.), raspberry canes (*Ru-*

Table 1. Insects employing plant tissue to transduce vibratory signals.

Insect	Plant	Context	Reference
Orthoptera			
<i>Neconema thalassinum</i>	leaf ?	courtship	Ragge (1965)
<i>Copiphora rhinoceros</i>	stem ?	courtship	Morris (1980)
<i>Neoconocephalus</i> spp.	stem ?	courtship	Whitesell (1969)
<i>Neoconocephalus ensiger</i>	stem ?	aggression	Gwynne (1977)
<i>Conocephalus nigropleurum</i>	stem ?	aggression	Morris (1971)
Mogoplistinae	leaf, stem ?	courtship, post-copulation	Love & Walker (1978)
<i>Oecanthus nigricornis</i>	<i>Rubus</i> spp. etc.	courtship, post-copulation	Bell (1979a)
<i>Oecanthus burmeisteri</i>	sunflower leaf	calling	Prozesky-Schulze et al. (1975).
Plecoptera			
Perlidae etc.	<i>Phalaris</i> spp.	courtship, calling	Rupprecht (1968)
Hemiptera			
<i>Oncopeltus fasciatus</i>	<i>Asclepias</i> spp.	mating	Walker (1979)
Homoptera			
<i>Dictophora europea</i>	leaf ?	calling	Strubing (1977)
<i>Euscelis incisus</i>	leaf ?	calling	Traue (1978)
Coleoptera			
<i>Golofa porteri</i>	palm leaf, stalk aggression		Eberhard (1977)
<i>Eusattus</i> spp.	bark ?	?	Tschinkel & Doyen (1976)
<i>Brentus anchorago</i>	bark ?	?	Johnson, L. K. (pers. comm.)
<i>Nothorrhina muricata</i>	bark ?	courtship	Faber (1953)
Diptera			
<i>Helius flavipes</i>	<i>Pilea</i> spp.	male assemblages	Zalom (1979)
<i>Euaresta</i> spp.	<i>Ambrosia</i> spp.	calling	Batra (1979)
<i>Liparia</i> spp.	<i>Phragmites</i> spp.	calling	Mook & Bruggemann (1968)
<i>Tephritis</i> spp.	<i>Senecio</i> spp.	calling	Tauber & Toschi (1965)

bus spp.), Canada thistle stems (*Cirsium arvense* L.), common cattail leaves (*Typha latifolia* L.), toadflax (*Linaria vulgaris* Hill), and goldenrod (*Solidago* spp.) were individually tested for their vibration transmission characteristics. The parts of all plants ranged from 30–35 cm in height with a

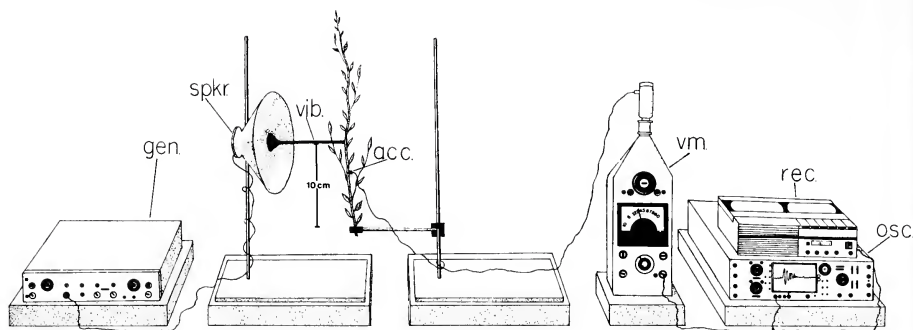


Fig. 1. Vibration generation and reception apparatus. gen., signal generator; spkr., speaker; acc., accelerometer; vm., vibration meter; rec., tape recorder; osc., oscilloscope.

base diameter not varying by more than 0.5 mm within species. The accelerometer was affixed to each plant at 180° to the probe at 2.5, 5, 7.5, 10, 12.5, and 20 cm from the top of the plant base clamp. Canada thistle stems required shaving for probe and transducer attachment. The probe attached to each plant 10 cm above the base clamp (Fig. 1).

Results and Discussion

Intraspecific plant vibration transmission variation as indicated by the standard deviation for each of the sample groups of 10 was small. Variation was usually greater further away from the probe, especially above (20 cm above base) (Fig. 2).

Orchard grass, raspberry cane, Canada thistle and goldenrod had nearly flat vibration transmission curves; while cattail and toadflax had rapid signal decay with greater distortion away from the probe (Fig. 2, 3). Tree crickets have never been observed by the author to mate on the latter two species. Tree crickets mate on all others (Bell, unpublished data). Cattail and toadflax also displayed a 'whip' effect on either side of the probe, i.e., the intensity of the signal increased momentarily before diminishing. In all plants excepting raspberry cane the deterioration of the vibrations was faster at the distal end.

Generally the vibrations were more distorted above the probe. Orchard grass, goldenrod and to some extent raspberry cane had a wave form resembling a sine wave with a slow decay, that is a vibration which is slowly dissipating energy over a narrow frequency band, i.e., 'ringing.' This was especially evident 2.5 cm above the base, thereby allowing these stiff stemmed plants to transmit vibrations further with more energy than more flexible stalked plants (Fig. 3).

Substrate vibrational communication in insects has certain advantages over acoustic, chemical and visual modalities. Predators are known or ex-

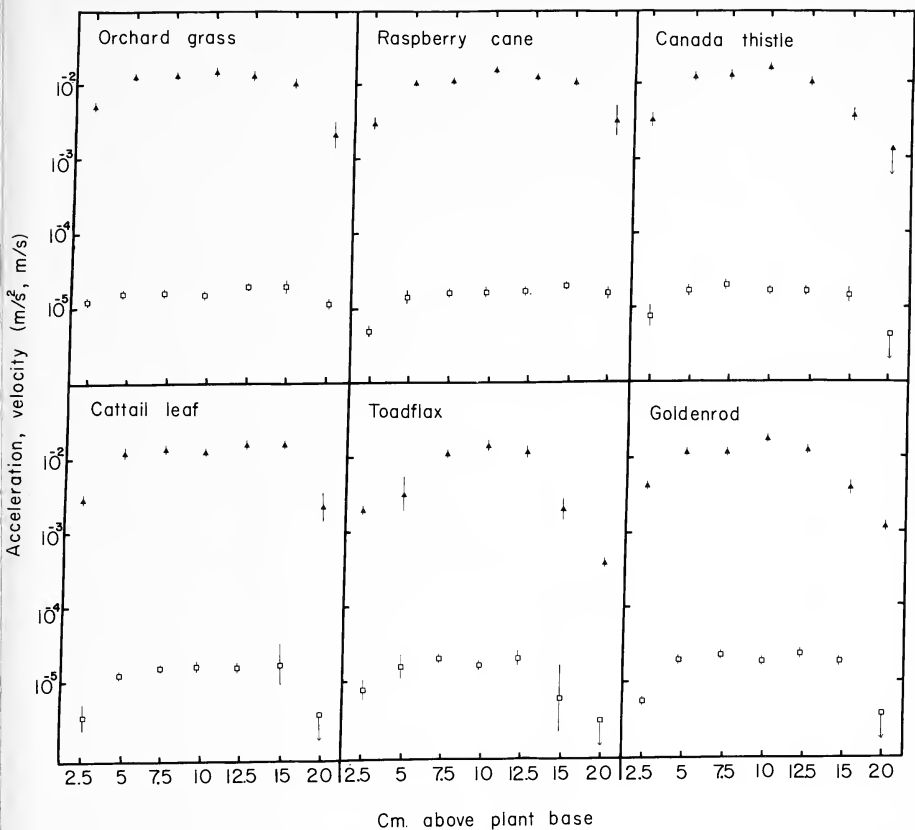


Fig. 2. Acceleration (▲), and velocity (□) of artificial vibrations. Each point represents the mean value of 10 plant specimens; bars equal 1 standard deviation, arrows indicate levels below meter sensitivity.

pected to use acoustic cues to locate insect prey (Bell 1979b; Walker 1964; Rentz 1975). Certain parasites display positive phonotaxis to singing insects (Cade 1975; Soper et al. 1975). Thus it may be advantageous for some insects to reduce the occurrence of acoustic displays. However, selection against acoustic displays will eliminate some opportunities for mate attraction. Substrate vibration signals have the ability of signalling only conspecific females, while avoiding detection by predators and other males at longer distances (Morris 1980; Walker 1979). Acoustic signalling is attenuated, absorbed, refracted, reflected and diffracted by variations in foliage mass, height, species composition, humus layer, soil, and atmospheric conditions (Linskens et al. 1976; Martin and Marler 1977; Wiley and Richards 1978). In addition the airborne sounds of some insects are highly directional (Leroy 1976; Paul and Walker 1979).

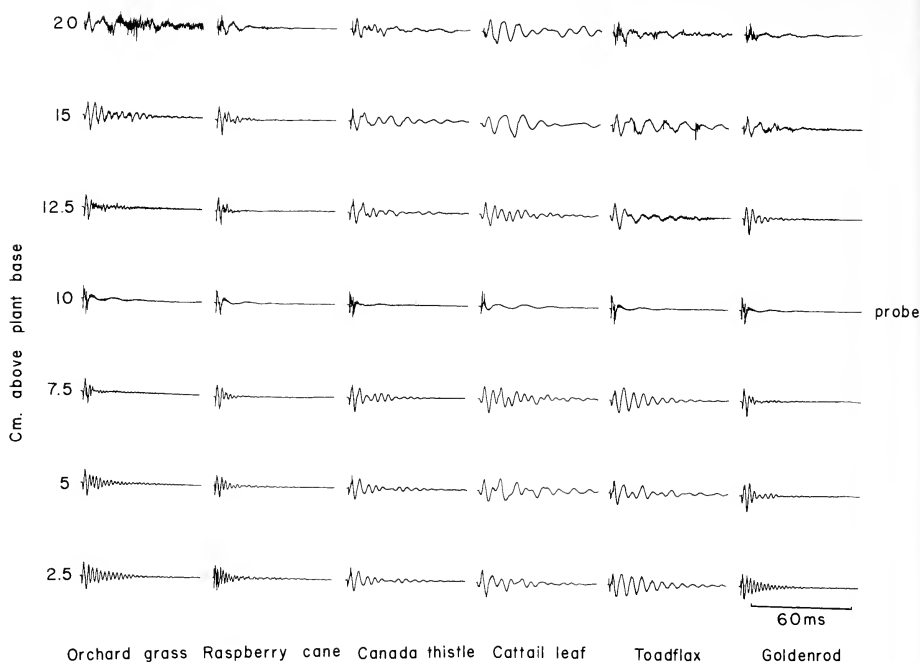


Fig. 3. Oscillograms of plant transduced artificial vibrations.

Just as in acoustic signalling, the directionality of pheromones will limit mate attraction to those within the broadcast field. Olfactory signalling has been shown to function in close range communication, e.g. (Paul 1976), but would be ineffective in unfavorable air currents.

Visual signalling is limited in many nocturnal insects and hampered diurnally in some by dense vegetation (Bell 1979a).

Vibrations on the other hand proceed along plant tissue in front of and behind the signaller in a predictable manner. In the absence of interfering (in contact) foliage there is less potential degradation of vibrations over short (<1 m) distances than of visual and chemical signals. Traue (1978) reported that vibrations from leafhoppers were perceived 90 cm away through plant stems. A vibratotactic function for *O. nigricornis* percussive vibration signals has been indicated by preliminary experiments. Also, the temporal integrity of the male tree cricket calling song is preserved as substrate transduced vibrations through the insects legs, and may assist orienting females (Bell, in progress).

The present study has demonstrated that the quality of vibration signals is dependent on the species of plant involved in transduction. Tree crickets and many other insects may exploit the vibration transmitting characteristics

of plants to signal conspecific mates. It is likely that as plants age, develop new structure, and succumb to changes in turgor pressure, they begin or cease to have vibrational characteristics that are advantageous for insect signalling. Selection would favor insects which could successfully select a substrate that could transmit their messages over greater distances without distortion and degradation. These individuals would increase their likelihood of attracting potential mates only. It is probable that certain plants such as orchard grass and raspberry cane are frequented by tree crickets because of their high 'Q' resonance qualities, which allow vibrational energy to be released over a narrow frequency band, thereby travelling further.

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Department of Zoology, Erindale College, University of Toronto, Mississauga, Ontario, L5L 1C6 Canada.

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OVER-EXPLOITATION OF LARVAL HOST PLANTS BY THE
BUTTERFLIES *HELICONIUS CYDNO* AND *HELICONIUS SAPHO*
(LEPIDOPTERA: NYMPHALIDAE: HELICONIINAE:
HELICONIINI) IN COSTA RICA?

Allen M. Young

Abstract.—I examined two small individuals of a larval host plant species (*Granadilla* sp.) of *Heliconius cydno* and *H. sapho* (Lepidoptera: Nymphalidae: Heliconiinae: Heliconiini) in northeastern Costa Rica to determine approximately the degree to which each one was utilized repeatedly. From the rather detailed conceptual framework and ecological studies of *Heliconius* butterflies I expected to find low clutch size and exploitation of fresh meristem for *H. cydno* and *H. sapho* as members of the “*Granadilla*-feeding” species group. The observations on one of the two plants agreed well with these expectations. On the other host plant individual, however, females of these species placed unusually high numbers of eggs on available fresh meristem. In subsequent observations when no apical meristem was present, no immature stages were found. The subtle interplay of many environmental factors, including shifting scarcities of fresh meristem on host plants, determines the intensity of oviposition on a particular plant.

Introduction

In some butterflies females searching for oviposition sites do not always accurately assess the suitability of a host plant individual in terms of larval growth and survival (Chew 1977). The pattern of egg placement on individual host plants by species which oviposit singly is often determined by the degree of patchiness of the host plant species (Chew 1977; Benson 1978; Young 1980). In many tropical butterflies such as *Parides*, females often place eggs on tiny seedlings of the host plant, clearly too small to support larval growth (Young, pers. obs., 1969–80, Costa Rica). But in some groups such as the Heliconiinae exploiting the Passifloraceae as larval host plants (Brower and Brower 1964; Gilbert 1975; Benson et al. 1976, and several other references) there appears to be careful assessment of host plant individuals by female *Heliconius* (Benson et al. 1976; Benson 1978). It is therefore of considerable interest to report here patterns of repeated exploitations of individuals of a host plant of *Heliconius cydno* in Costa Rica. An incidence in which a related species, *Heliconius sapho*, overexploited one of the host plants used by *H. cydno* is also reported.

Materials and Methods

I observed female *H. cydno* deposit eggs on two immature individuals of *Granadilla* in northeastern Costa Rica. I also discovered a large number of eggs of *H. sapho* on one of these plants. The general locality is a 4,000-acre farm complex about 8 km north of La Virgen, Heredia Province, a region within the premontane tropical wet forest zone (220 m elev.) (Holdridge 1967). Information on the biology of *H. cydno* and *H. sapho* in Costa Rica has been summarized elsewhere (Smiley 1978; Young 1973, 1978). Both species are abundant along borders of forest.

The initial observations of *H. cydno* at one host plant were made on February 14, 1977. I marked the location of the plant, took notes on its size and appearance (number of fresh and old leaves, herbivore damage, etc.), and returned many times until March 6, 1977 to make observations on the eggs and larvae present. I examined the patterns of larval feeding and any interactions among larvae.

The specific locality of the first plant is "Finca La Tigra," mixed cacao (*Theobroma cacao* L.) plantations and various stages of forest succession. On August 3, 1978 I discovered *H. cydno* ovipositing on another individual of the same plant species but this time at "Finca El Uno," an area of cacao, *Hevea* rubber, and strips of young secondary succession about 5 km from the "La Tigra" site. I recorded the immature stages present and made observations until August 8. The location of this plant was marked and I returned to examine for the presence of *H. cydno* or other *Heliconius* in five additional periods: December 1–4, 1978; March 12–20, 1979; June 30, 1979; September 11, 1979; and February 21–22, 1980. Each time I recorded the appearance of the plant, noting presence of fresh leaves and other features. Upon returning to the site of the "El Uno" plant on June 13, 1980 I noted the presence of new meristem and many eggs scattered on it. Observations were made through July 2 during which it was determined that the species was *H. sapho*. I observed the abundance of larvae and their distribution on the plant.

Results

The host plant is an immature *Granadilla*, a subgenus in the passifloraceous subfamily Laurifoliae, which consists chiefly of small, erect plants without tendrils (Dr. K. S. Brown, Jr., pers. comm.). The plant is possibly *Passiflora guazumaefolia*. At this locality *H. cydno* oviposits on at least one other *Passiflora*, this time a vine, *P. vitifolia* with different taxonomic affinities within the family (Young 1978). Owing to the tentative nature of host plant identifications I refer to them as "*Granadilla* A" (La Tigra) and "*Granadilla* B" (El Uno).

"*Granadilla* A".—This individual was found in a light gap along a well-

shaded footpath (Fig. 1A) in disturbed primary forest and at the time of its discovery it had four fresh leaves (new meristem) (Fig. 1B). The plant was about 0.25 m tall (Fig. 2A) with few signs of herbivore attack to both older leaves or fresh meristem. At 1130 hours on February 14, 1977 one "fresh" female *H. cydno* was noticed inspecting the plant and two eggs were placed on it within a 20-minute period. The first egg was deposited at 1140 hours next to the midrib on the ventral side of one of the apical fresh leaves; a second egg was already present on the same leaf. Another egg was placed on the petiole of a fresh leaf (Fig. 2B) ten minutes later. No additional eggs were found. Judging from the white color of the egg already present, this egg was probably a few days old and possibly not from the same female witnessed placing two eggs. Fresh eggs of *H. cydno* are yellow (Young 1973). This plant had a total of ten leaves, including the fresh ones. No other *Heliconius* eggs or larvae were found on the plant.

The following day the older egg hatched and matched the general description for the first instar of *H. cydno* (Young 1973). This larva rested on the tip of the fresh leaf bearing the two eggs. Later that day one of the other eggs disappeared, possibly the result of predation by ants or cannibalism by the larva present. At 1530 hours that day, an ant approached the larva and it dropped on a silken thread from the leaf. Several small reddish-brown (unidentified) ants were seen at the conspicuous extra-floral nectaries on the petiole of one of the lower yet fresh leaves. On the following day (February 16) the larva had eaten away a strip of fresh leaf tissue on the leaf bearing the surviving egg. Later that day a new egg was found on the petiole of another fresh leaf.

The first instar begins feeding from the edge of a fresh leaf, cutting deep notches into the tissue and eventually reaching the midrib area. This larva stayed on the same fresh leaf for all five instars, completing molt cycles on it and eventually developing a feeding pattern in which entire sections of the leaf are chewed away (Fig. 3A, B). Prior to pupating it eventually moved onto two other fresh leaves at the top of the plant and attaining a body length of about 35 mm. The two additional eggs present disappeared and this larva was the only one on this plant for the study period.

I noticed that the larva fed both day and night, but intermittently and with no consistent pattern. The larva eventually pupated on an older leaf of the host plant. It is estimated that the larvae ingested approximately 140 mm² of fresh leaf tissue by the time of pupation. Older leaves were not consumed. The portion of fresh leaf tissue consumed represents about 60% of the total amount of fresh leaf tissue available on the plant during the study period. No additional fresh leaves were produced during this period. Other than the total of four eggs counted in the first few days, no additional eggs were found thereafter.

"*Granadilla B*".—This plant was discovered again as the result of an *H.*



Fig. 1. (A) The forest habitat understory where "*Granadilla A*" was discovered. (B) "*Granadilla A*" showing the fresh meristem (stem and leaves) contrasting in shade from older leaves.

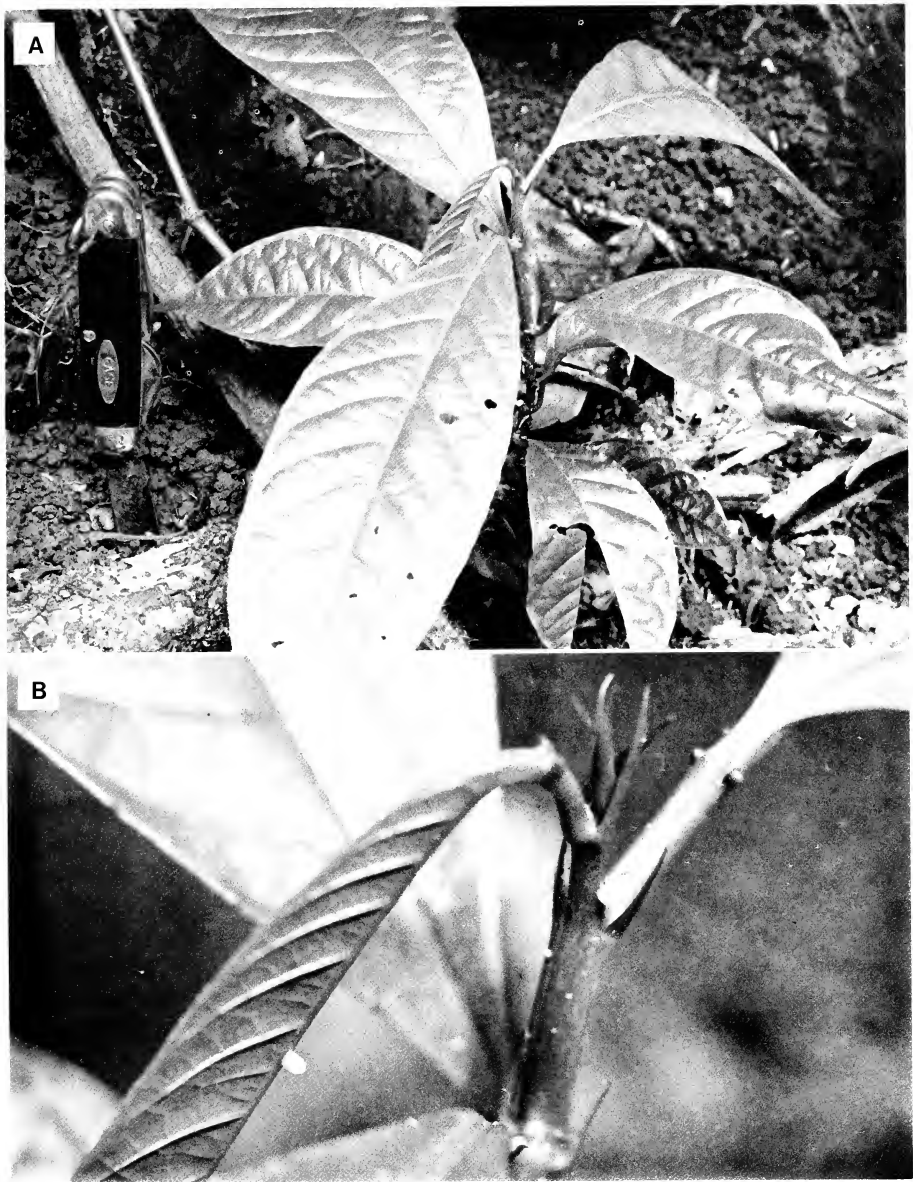


Fig. 2. (A) The fresh leaves and other parts of meristem on "*Granadilla A*"; note few signs of any appreciable herbivore damage. (B) Positions of two eggs of *Heliconius cydno* on the fresh meristem of "*Granadilla A*"; note that one egg is near the midrib of a young leaf while the second egg is at the base of the petiole; note the conspicuous extrafloral nectaries on a petiole to the right.

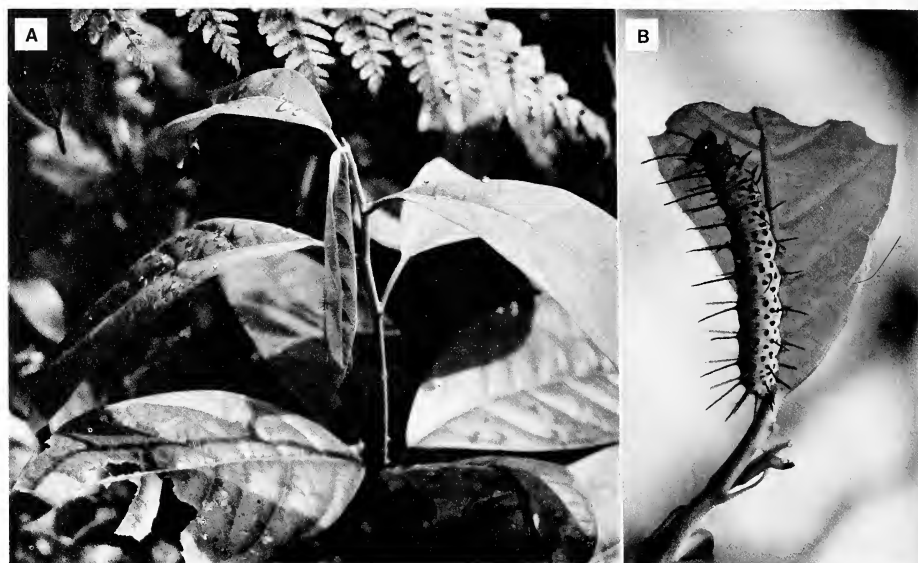


Fig. 3. (A) Note the damage from feeding by the larva of *H. cydno* on the fresh leaf in the lower left. (B) Fourth instar larvae of *H. cydno* with typical pattern of damage to a fresh leaf on "Granadilla A".

cydno female inspecting it (August 3, 1978, 0930 hours). It was found in a strip of dense herbaceous vegetation along a shaded trail within a cacao plantation. The plant was about 0.30 m tall when discovered and of a total of 12 leaves present six were fresh meristem. As with the first plant, the fresh leaves are easily distinguished from the older ones by their light green color and soft texture. The plant was actually a sucker shooting up from a thick woody stem.

A tattered female of *H. cydno* deposited a total of 15 yellow eggs on the apical stem of this plant (Fig. 4A) within a ten-minute period on the morning of discovery. The butterfly made four different visits to the plant, after flying off and fluttering through nearby vegetation before returning to deposit more eggs. The eggs were placed singly (Fig. 4B). Within five days after oviposition the folded apical region of the host plant had "leafed out" (Fig. 4C), making a spectacular display of bright yellow eggs packed into a relatively small area of fresh leaflets and stem. The result is a "loose" clustering of many eggs on the apical and fresh portion of the plant (Fig. 4C). An examination of the plant following the oviposition revealed no additional eggs or larvae, although an empty pupal shell of *Heliconius* was found on a seedling adjacent to the host plant. At the time of oviposition a raiding column of army ants (*Eciton* sp.) passed within a few centimeters of the host plant but did not affect oviposition.



Fig. 4. (A) *Heliconius cydno* in the act of placing several eggs on the fresh meristem of "Granadilla B". (B) Egg of *H. cydno* on the fresh petiole of "Granadilla B". (C) The distribution of 15 eggs of *H. cydno* on the unfolded fresh leaflets and stem of "Granadilla B".

Egg number remained the same for the first four days following the burst of oviposition activity. By the fifth day, however, there were only eleven eggs and no first instar larvae to account for the remaining four. One of the remaining eggs was shriveled up. The same plant was re-examined in December and two larvae (second instar and third instars) of *H. cydno* were present on the plant (December 1, 1978). No eggs were present. At this time the plant was about 30 cm tall with roughly 50% of the biomass being fresh. The two larvae occupied different leaves. Several ants were seen patrolling the apical area of the plant on two days following the discovery. For the period March 12–20, 1979 fresh leaves were entirely absent from the plant and no *Heliconius* early stages were found. The plant was about the same size as it was in the previous December although no new growth was present. I noticed three fresh adults of *Philaethria dido* (Heliconiinae) flying in

the vicinity of the plant on one day. The general condition of the herbaceous vegetation was lush at this time. The plant was in the same general condition on June 30, 1979 and no early stages of *H. cydno* were found on it. The plant was briefly observed in September 1979 and February 1980 and again there was no new growth and no signs of *H. cydno* on it.

The plant was re-examined on June 13, 1980 at which time it had fresh meristem about 40 cm high and bearing eight full-sized and folded leaflets. The bottom woody part of the plant had ten old leaves. A total of 20 *Heliconius* egg shells were found scattered on the fresh leaflets and there were 14 second instar larvae in a tight aggregation on one leaflet. No unhatched eggs were present. By June 16 only eight larvae remained and the leaflets were now completely unfolded and the egg shells gone. No observations were made until June 29 at which time it was discovered that all of the fresh meristem had disappeared and that only one chrysalis was present on an older leaf. A thorough search of the surrounding vegetation within a four-meter square area failed to turn up additional chrysalids. The chrysalis hatched July 2 and proved to be *H. sapho*.

Discussion

Heliconius cydno and *H. sapho* are species in the "melpomene" group, being closely allied with other species such as *H. pachinus*, *melpomene*, and *heurippa* (Brown and Mielke 1972; Benson 1978). The species are classified as laying medium to large eggs, solitary meristem feeders as a larvae, and generally requiring large host plant individuals (Benson 1978). The clutch size is generally small (Benson 1978) and a species such as *H. melpomene* places eggs singly on subterminal leaflets and young tendrils (Alexander 1961). The usage of meristem tissues by *Heliconius* species comprises a major aspect of the radiation of the group (Benson et al. 1976). *Heliconius cydno* is oligophagous while the allied *H. melpomene* in Costa Rica is monophagous (Smiley 1978). The species oviposits on at least one non-*Granadilla* host plant at the site of the present study (Young 1978) as it does in a Costa Rican mountain wet forest site (Young 1973). *Passiflora vitifolia* is a common and widespread host plant of *H. cydno* and several other *Heliconiinae* at the study site (Young 1978) as well as at nearby "Finca La Selva" (Smiley 1978). Twenty-seven species of *Granadilla* are used by at least eight species in the "transitional" and *melpomene* groups (Benson et al. 1976).

Many species in the "Granadilla-feeding" group (Smiley 1978) place eggs singly on fresh meristem and the larvae feed primarily on these tissues (Benson et al. 1976). The availability of fresh meristem is a limiting factor in the populations of some *Heliconius* species (Benson 1978; Smiley 1978). The butterflies are adapted for searching for and placing eggs on this portion of the individual host plant (Gilbert 1975).

Assuming that the observed host plant was indeed *P. guazumaefolia* and the fact that many species in the *Granadilla*-lineage of the Passifloraceae have conspicuous extrafloral nectaries that attract ants (Gilbert 1975; Benson et al. 1976) the observed loss of eggs, apparently from ant predation, is not unexpected. It is also known that some species of *Granadilla* possess stipules resembling *Heliconius* eggs and larvae (Benson et al. 1976) thus discouraging repeated oviposition in *Heliconius* which place eggs singly on meristem. Such factors reduce the likelihood that a female *Heliconius* will oviposit repeatedly on the meristem of a particular individual of the host plant species available in the habitat. The species of *Heliconius* exploiting such host plants generally have aggressive larvae so that there is usually no more than one larva per meristem (Benson et al. 1976).

Yet "*Granadilla* B" presents a different picture. The observed placement of fifteen eggs on a single fresh meristem by *H. cydno* is a notable departure from the expected clutch size. The usual clutch size of this species is small (1-3 eggs per plant) (Benson 1978; Young 1978). Presumably the plant was too small to support all of the larvae. Perhaps ant predation and aggressive interactions among the larvae would have taken a heavy toll thus reducing effective clutch size considerably. The apparent placement of 20 eggs on fresh meristem of the same plant by *H. sapho* and the subsequent dwindling of larvae in this gregarious species is a further indication of the interaction of reduced food supply and possibly predation as reducing larval numbers in this species. Presumably the eggs were placed in a relatively loose cluster at an even earlier stage in the unfolding of the fresh meristem. The data suggest that the larvae defoliated the plant of the fresh meristem and that only a portion of them survived.

Why should some *Heliconius* "invest" about five times the expected number of eggs in a small individual of *Granadilla*? The answer is clearly beyond the scope of this paper, yet it is interesting to suggest one explanation based upon the concept of limiting resources affecting the butterfly at the study site. The consecutive choices by a female butterfly searching for oviposition sites is influenced greatly by the spatial distribution of suitably host plant individuals (Chew 1977; Benson 1978; Young 1980). If host plant individuals are very patchy and concealed, one might expect exploitation of alternative host plant species or more intense exploitation of the individual host plant when encountered. Although several species of host plant might be available in the habitat, their suitability for oviposition by meristem specialists such as *H. cydno* and *H. sapho* is determined largely by the availability of fresh meristem tissues. My general impression of the relative abundance of *P. vitifolia* to *P. guazumaefolia* at the locality of the present study is that the former species is far more abundant. There seems to be a greater number of patches per unit of habitat and the biomass of each patch is considerably larger. Whether or not *H. cydno* and *H. sapho* exhibit a physiological preference for one species over the other is not

known, although one study showed that the *H. cydno* exhibits approximately equal oviposition frequency on several host plant species in different subgenera (Smiley 1978). Therefore the differential in terms of actual host plant usage in the wild is probably largely determined by relative patch structures among host plant species and the availability of fresh meristem among the species.

The scarcity of *Granadilla* (*P. guazumaefolia*) coupled with perhaps reduced availability of fresh meristems on other host plants such as *P. vitifolia* may induce repeated oviposition on small patches of those host plants with fresh meristem. Chew (1977) noted that there is sometimes considerable discrepancy between oviposition behavior and the suitability of the chosen host plant individual for larval growth. I have noted similar situations in *Parides* (Papilionidae) ovipositing on *Aristolochia* seedlings and *Morpho peleides* oviposit on tiny seedlings of *Machaerium seemanii* in Costa Rica.

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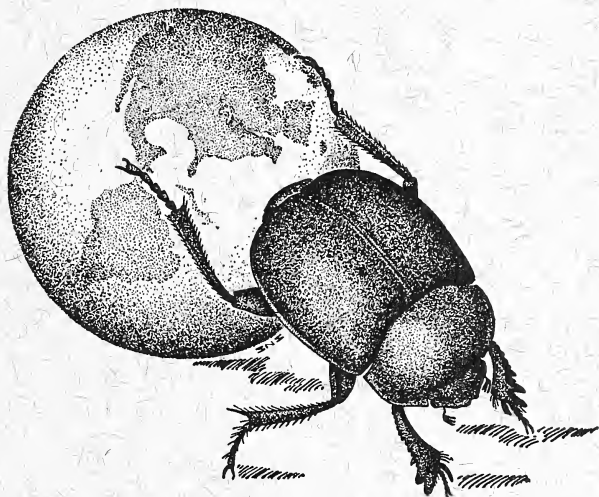
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THE SOUND-PRODUCING STRUCTURES OF SOME PRIMITIVE
PENTATOMOIDEA (HEMIPTERA: HETEROPTERA)

Carl W. Schaefer

Abstract.—The Cydnidae and Thyreocoridae have a small stridulitrum on the under side of the hindwing's postcubitus. The plectrum is a striated lima on the first tergite. Possession of the stridulitrum and plectrum is probably plesiomorphic in a complex of primitive Pentatomoidea.

The Thaumastellidae (a member of the complex) also have a stridulitrum, near the postcubitus of the hindwing, and a similar plectrum. Some Scutelleridae and Tessaratomidae have a similar stridulitrum. Other morphological features ally these two families with—but are insufficient to warrant including them in—this complex of primitive pentatomoids.

Members of the families Cydnidae and Thyreocoridae, both primitive in the Pentatomoidea, possess a stridulitrum on the lower surface of the postcubital vein of the hindwing (Dupuis 1953; Leston 1954, 1957; Lawson and Chu 1971; Draslar and Gogala 1976). The stridulitrum is small (less than a millimeter long) and composed of cuticular ridges. The part of the vein that bears it is raised, darkened, and more heavily sclerotized than the rest of the vein. The plectrum across which presumably the stridulitrum strums, is a striated lima on the anterior edge of the first abdominal tergite (Draslar and Gogala 1976). Muir (1907) and Leston (1954) discuss the functioning of the stridulitrum and plectrum, and Gogala (several references: see 1978) describes and characterizes the sounds produced and discusses their functions.

The possession of the stridulitrum by these families assumes greater interest now that they appear to be part of a larger complex of primitive Pentatomoidea (Thaumastellidae, Plataspidae, Cyrtocoridae, Megarididae, Canopidae, and perhaps Lestoniidae [Schaefer, in preparation]), and now that Stys (1964) has described a similar stridulitrum in the Thaumastellidae. Moreover, some (but not all) members of two other families, not members of the complex, also have a postcubital stridulitrum. Some, perhaps most, Tessaratomidae have such a stridulitrum (Muir 1907; Dupuis 1953, Au 1969), and so do certain Scutelleridae (Au 1969). Spermathecal features ally parts of these families to the group of primitive pentatomoids (Schaefer, in preparation).

The distribution of the postcubital stridulitrum is clearly important. Unfortunately, when Leston (1957, p. 372) wrote that he had found it in "a further twenty-five genera" of Cydnidae, he did not name them. His concept (1961) of the Cydnidae differs from the more generally accepted one of Froeschner (1960), and one cannot be sure if Leston found such a striduli-

trum in the Amnestinae, the Scaptocorinae, or the Garsauriinae. Moreover, his description (1954) of the plectrum in several of these bugs requires some amplification.

Here I describe briefly the stridulitrum in the Cydnidae (except Garsauriinae, of which I had no representatives) and Thyreocoridae, and discuss the cladistic significance of its presence in these families and the Thaumastellidae.

Results

The presence and some characteristics of the postcubital stridulitrum are given in Table 1.

The size and number of teeth of the stridulitra of all families vary considerably, as does their "packing"; but the ridged form of the teeth and—more importantly—the overall shape of the stridulitrum itself, are constant; although, in *Tessaratoma*, the teeth are more chisel-like and less ridge-shaped. Variation probably occurs between sexes and among species, as Draslar and Gogala (1976) have shown for two species (of different subgenera) of *Sehirus*.

As Au (1969) remarks, the possessors of the stridulitrum can be placed into either of two groups: those with many teeth (Scaptocorinae, Amnestinae, Thyreocoridae, and Scutellerini) and those with few teeth (Cydninae, Sehirinae, Thaumastellidae, and Tessaratomidae) (see Table 1).

The plectra of all species studied, except those in the Thaumastellidae and Scutelleridae, is a very small striated lima located sublaterally on the anterior border of the first tergite. Its position does not change from species to species, although its development does (see scanning electron micrographs in Draslar and Gogala 1976); the striations in *Amnestus* are so fine as to be invisible except at high (200×) magnification.

Leston (1954) places the plectrum in the Sehirinae on the third metathoracic phragma (scutum 3), but admits there is some confusion about the naming of the sclerites in this region. In his figure 4, he placed the plectrum, correctly, on the anterior border of the first tergite, and not on phragma 3.

As in the others, the plectrum of *Tessaratoma papillosa* is on the first abdominal tergite, not on a "sclerite . . . between the metathorax and first abdominal segment" (Muir 1907, who misnumbered the segments; an error repeated by Au 1969). The plectrum is paired and resembles those of the Cydnidae and Thyreocoridae closely, although it is more medially situated than are theirs.

The plectrum of the Thaumastellidae closely resembles those above, but occurs on the second abdominal tergite, not the first.

The scutellerid plectrum (in *Callidea duodecimpunctata*) is as Au (1969) describes and figures it for *Scutellera nobilis* Distant: "a heavily sclerotized

Table 1. Characteristics of the stridulitrum of some primitive Pentatomoidea.

Species	Total teeth	No. teeth/mm	Jugal hole	Reference
Cydnidae: Cydninae				
<i>Aethus indicus</i> (Westwood) (♀)	18	65	no	this paper
<i>A. indicus</i> (♀, ♂)	17-20	—	—	Leston, 1954
<i>Pangaeus bilineatus</i> (Say) (♀, ♂)	30-40	130*	no	this paper
		(45/mm distally, 190/mm proximally)		
<i>Microporus obliquus</i> Uhler	30-35	90/mm distally; 250/mm proximally	no	Lawson & Chu, 1971
Cydnidae: Schirinae				
<i>Sehirus cinctus</i> (Palisot de Beauvois) (♀)	12-15 or 32*	72-75	no	this paper
<i>Sehirus bicolor</i> (L.)	17-19	—	—	Leston, 1954
<i>Dismegistus fimbriatus</i> Thunberg	16-18	50 (estimate)	—	Leston, 1956
Cydnidae: Scaptocorinae				
<i>Scaptocoris divergens</i> Froeschner (♂)	84	150	no	this paper
<i>Atarsocoris gisellae</i> (Carvalho) (♂)	65	150	no	this paper
Cydnidae: Amnestinae				
<i>Amnestus spinifrons</i> (Say) (♂)	70	380	no	this paper
Thyreocoridae				
<i>Thyreocoris scarabaeoides</i> (L.) (♂)	60	250	?	this paper
<i>Corimelaena pulicaria</i> (Germar) (♂)	ca. 200	ca. 700	?	this paper
<i>Galgupha ovalis</i> (Hussey)	ca. 100	ca. 200	yes	Lawson & Chu, 1971
Thaumastellidae				
<i>Thaumastella aradoides</i> Horvath	44	—	—	Stys, 1964
Scutelleridae				
<i>Callidea duodecimpunctata</i> F. (♀, ♂)	300	250	no	this paper
Tessaratomidae				
<i>Tessaratomia javanica</i> Thunberg (♂)	12-15	10	no	this paper
Cyrtocoridae				
<i>Cyrtocoris laceratus</i> Herrich-Schaeffer	no stridulitrum			this paper
<i>C. sp.</i>	no stridulitrum			Au, 1969
Plataspidae				
<i>Coptosoma cribraria</i> (F.)	no stridulitrum			this paper
<i>Brachyplatys vahllei</i> (F.)	no stridulitrum			Au, 1969
Megarididae				
<i>Megarid sp.</i>	no stridulitrum			this paper

* Two specimens; possibly sexually dimorphic.

file-like sclerite"; however, it is not on the "anterolateral area of the first abdominal tergum" but (as indeed she figures it), single and medial on the tergum. The plectrum in both *Scutellera* and *Callidea* is much larger than it is in the Thaumastellidae, Cydnidae, Thyreocoridae, and Tessaratomidae; in those scutellerids it occupies the medial fifth of the first tergite's anterior border. Its striations run front-to-back, not side-to-side, as do those of the other four families.

Leston (1957) remarks that the jugal wing area of the Cydnidae is smaller than that of the Thyreocoridae and, when folded under, does not overlap the stridulitrum and intervene between it and the plectrum. Therefore, the cydnid jugal area lacks the hole McAtee and Malloch (1933), and Leston (1954), believe to characterize the Thyreocoridae, and Lawson and Chu (1971) describe for *Galgupha*. I too have not seen such holes in the Cydnidae (Table 1), but Draslar and Gogala (1976) show that they accommodate individual stridulitral teeth in this family, and are so small as to be undetectable at the magnifications usually used in dissecting. Muir (1907) mentioned abrasions in this region of the *Tessaratomya papillosa* Thunberg wing. Au (1969) did not report holes in the Scutelleridae nor did I find them in *Callidea duodecimpunctata*.

Discussion

There are three groups of pentatomoids: those without the postcubital stridulitrum, those with it and a first-tergal plectrum, and one family (Thaumastellidae) the homology of whose stridulitrum and plectrum is problematic.

Those families lacking the PCu stridulitrum include the Pentatomidae, Urostylidae (Urostylinae and Saileriolinae), Acanthosomatidae, some Scutelleridae, and some Tessaratomidae (unpublished observations); other families probably lack it, but have not been studied.

The location and structure of both the stridulitrum and the plectrum are so similar in the Cydnidae and Thyreocoridae, that it seems unlikely to have evolved more than once: the character unites the two families, as Dupuis (1953) and Leston (1954 and elsewhere) have emphasized. However, the presence of both structures in some Tessaratomidae—a group in other respects not close to those two families—weakens the argument that the common possession of these structures requires close common ancestry of their possessors.

The stridulitrum of *Thaumastella aradoides* Horvath (Thaumastellidae) is just anterior to, not on, the postcubitus (Stys 1964); nevertheless, the general position of this stridulitrum, and its structure, suggest strongly it is homologous with those of the Cydnidae and Thyreocoridae. The stridulitrum of the strongly brachypterous *T. namaquensis* Schaefer and Wilcox may be at the second-third tergal border, but this is uncertain (Schaefer and

Wilcox 1971). However, the plectra of both species are alike, a small striated area not on the first tergite but on the second.

Despite these differences in position, I believe the thaumastellid stridulitrum (of *T. aradoides*) and plectra to be homologous with those of the Cydnidae and Thyreocoridae, because the structures are so similar in all three families. Accepting this position argues for the inclusion of the Thaumastellidae in the unit containing the other two families. However, pentatomoid families phylogenetically closer to the Thaumastellidae than these two lack the stridulitrum and the plectrum. Therefore, I consider possession of a postcubital stridulitrum and abdominal plectrum to be an autapomorphy helping to define a complex of primitive Pentatomoidea, a complex defined also on other characters (Schaefer, in preparation). Within the complex the character is symplesiomorphic, and the stridulitrum and plectrum have been lost in several members (Table 1); but loss has not occurred so frequently (only three times) as to vitiate my argument that stridulitrum and plectrum have indeed evolved only once.

The postcubital stridulitrum occurs in some 12 genera of the Scutelleridae (Au 1969), and so presumably does the first-tergal plectrum, although Au did not check for its presence in all genera. Ten of the 12 genera belong to the Scutellerini, as defined by Schouteden (1904), who treats the scutellerids as a subfamily, not a family. One exception is *Steganocerus*, considered a member of the Scutellerinae: Sphaerocorini until Leston (1952) transferred the genus to his more restricted Scutellerini (a fact apparently overlooked by Kumar [1965]). The other exception, *Chiastosternum*, is listed next to *Steganocerus* by Schouteden in his list of Sphaerocorini.

The stridulitrum appears not to occur in the other scutellerid subfamilies, the other scutellerine tribes, and certain members of the Scutellerini (*sensu* Leston) itself.

In spite of the differences between the plectrum of the Scutellerini and those of the Cydnidae, Thyreocoridae, and Tessaratomidae, the placement of all plectra on the first abdominal tergite indicates, tentatively, they are homologous. That they are in fact homologous must await a cladistic study of the Scutelleridae *vis a vis* these other pentatomoids, a study based on other characters.

I do not believe either the Scutelleridae or the Tessaratomidae belong to the group of primitive Pentatomoidea of which the Cydnidae, Thyreocoridae, and Thaumastellidae are members, although some scutellerids (and possibly some tessaratomids) share some spermathecal characteristics with some members of the group (Schaefer, in preparation). It seems to be possible that the two families evolved from members of the primitive group, and that the stridulitrum and plectrum are plesiomorphic in the Scutelleridae and Tessaratomidae. In this regard it is significant that Kumar (1965) considers the Scutellerinae (=Scutellerini of Schouteden) to be primitive with

respect to female genitalia, and Au (1969) considers their hindwing ventation primitive; for it is in this subfamily that stridulitrum and plectrum are found.

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Systematic and Evolutionary Biology Section, Biological Sciences Group, University of Connecticut, Storrs, Connecticut 06268.

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THE HOUSE-FLY MYCOSIS CAUSED BY *ENTOMOPHTHORA*
MUSCAE: INFLUENCE OF RELATIVE HUMIDITY ON
INFECTIVITY AND CONIDIAL GERMINATION

John Paul Kramer

Abstract.—Studies on the effects of various relative humidities on the infectivity of *Entomophthora muscae* conidia showed that *Musca domestica* exposed to conidial showers falling through atmospheres with relative humidities ranging from zero to 100% acquired fatal infections. Studies on the germination of conidia held at various humidities showed that the fungus produces long germ tubes only from secondary conidia at 100% R.H. These results suggest that *E. muscae* can be transmitted within fly populations during periods of dry-cool weather, and that the relative humidity within the boundary layer surrounding the fly's body is at or near the saturation point. Temperature maintained during the studies was $21 \pm 3^{\circ}\text{C}$.

Introduction

The mycosis of the house fly caused by *Entomophthora muscae* has been recognized for more than a century. One factor that undoubtedly influences the occurrence of this disease in populations of *Musca domestica* and other species is atmospheric humidity. Wilding and Lauckner (1974), in a review of the literature pertaining to this subject, noted that epizootics occur mainly in wet and cool periods but are known from dry and warm ones as well. In their own studies these authors found little correlation between atmospheric conditions and the incidence of the disease in the field. Berisford and Tsao (1974) also found no striking relationship between the incidence of *E. muscae* infections and weather conditions. Baird (1957) noticed accidental transmission of *E. muscae* among caged flies held in the laboratory at about 23°C and a relative humidity of 50%; for reasons unknown the fungus was not transmissible after the cultures of flies were transferred to another room with similar atmospheric conditions. I (Kramer, 1980) reported successful transmission of *E. muscae* to house flies held in humid chambers at $14\text{--}27^{\circ}\text{C}$ and no transmission of this pathogen to flies held in a dry chamber at $21\text{--}27^{\circ}\text{C}$. I also noted that many conidia held on glass slides in a humid chamber germinated whilst few conidia held under similar circumstances in a dry chamber did so. The present study defines with greater precision the effect of humidity in the ambient environment on the infectivity of *E. muscae* conidia and on the germination of *E. muscae* conidia.

Materials and Methods

I collected about 30 living cluster flies *Pollenia rudis* from the window panes of a heated building where a natural epizootic of the mycosis was in progress on December 8, 1979. Cluster flies from this collection dying of the disease over the next six days served as a source of inoculum used to establish *in vivo* cultures of *E. muscae* in house flies by a method described previously (Kramer 1980). Conidia-bearing cadavers from these cultures served as the source of inoculum for the studies described herein. Primary conidia were uniformly bell-shaped with an apical point while the smaller secondary conidia lacked the apical point; clearly the fungus was *E. muscae* (see MacLeod et al. 1976).

Infectivity Tests.—Batches of 20 to 25 young healthy flies were placed in cylindrical, clear plastic cages (height 35 mm, width 30 mm) having two large mesh-covered windows and mesh-covered tops and bottoms. Three fresh cadavers of *M. domestica* with *E. muscae* infections were affixed with petrolatum to the inner surface of small plastic dishes. A dish bearing cadavers was placed over each cage to allow the conidia discharged to fall through the mesh-covered top into the cage of flies. These cages with dishes were placed in glass battery jars tightly covered with layers of polyethylene wrap and waxed paper. The relative humidities maintained in these chambers are given in Table 1. After 24 hours the test flies were fed honey and the dishes with cadavers were removed. After an additional 24 hours the flies were transferred to glass-covered carton cages, and each cage was provisioned with a water bottle and a mixture of dried milk and sugar. These cages were held at $21 \pm 3^\circ\text{C}$ and 45% R.H. with a 18:6 photoperiod. The cages were checked for infected flies at daily intervals. The findings are given in Table 1.

Germination of Conidia.—Three or four freshly dead or dying house flies with *E. muscae* infections were affixed to the inner surface of small plastic dishes as described above. These dishes were suspended over glass cover slips in closed chambers maintained under the conditions given in Table 2. Twenty-four hours later the slips, mounted in Colley's solution (Colley, 1925), were examined microscopically. The patterns of germination observed are given in Table 2.

Humidities.—The relative humidities within the tightly closed jars were achieved with saturated solutions of the following compounds: Pyrocatechol (94%), KCl (85%), NaCl (75%), NaNO_2 (65%), glucose (55%), KNO_2 (48%), NaI (38%), and NaOH (6%). Since a means to measure the actual humidities was not available, the percentages were taken from a table given by Winston and Bates (1960). Distilled H_2O provided a relative humidity of 100%; anhydrous CaCl_2 in a dry jar maintained a relative humidity at or near zero percent.

Table 1. Infectivity of *Entomophthora muscae* conidia falling upon healthy *Musca domestica* held at various relative humidities at 21°C.

Relative humidity	No. flies at risk	Post-exposure days with percentage dying of infection					Total percentage fatally infected
		1-4	5	6	7	8	
100	20	0	5	50	45	0	100
94	20	0	5	70	25	0	100
85	21	0	0	86	14	0	100
75	23	0	0	61	30	9	100
65	24	0	0	38	29	12	79
55	22	0	10	36	36	0	82
48	20	0	0	60	0	0	60
38	20	0	10	50	20	0	80
6	21	0	14	33	10	14	71
0	15	0	0	7	13	0	20

Results and Discussion

Flies exposed to conidial showers falling through atmospheres with relative humidities ranging from zero to 100% acquired fatal *E. muscae* infections (Table 1). At relative humidities of 75% and above all flies at risk became infected, while at 65% R.H. and below some flies apparently escaped infection. Why some flies did not acquire the infection is unclear. Inherent resistance is probably not the explanation, since uninfected survivors from these tests later proved to be quite susceptible when exposed to conidial showers at 75% R.H.

Primary conidia were produced and discharged from cadavers of flies held at relative humidities ranging from zero to 100%. Conidial showers from cadavers in atmospheres with low relative humidities (6 and 38%) were markedly scanty compared to those from cadavers at 55% R.H. or higher. That some conidia are produced at 0% R.H. suggests that the cadaver of a well-nourished fly supplies moisture adequate for the development of a few of these asexual spores. The data in Table 2 show that some primary conidia produced secondary conidia at all humidities considered. Often these secondary conidia developed small lateral bulges. Other secondary conidia produced germ tubes about as long as a secondary conidium at humidities of 48% and above. Only at 100% R.H. were germ tubes more than twice as long as a conidium formed from secondary conidia. These long tubes were often branched and sometimes two or more tubes arose from one conidium. The significance of these variations is unknown. Long tubes completely separated from the secondary conidium of origin were observed only at 100% R.H. In no instances were forms clearly identifiable as tertiary conidia observed in any of the slide preparations.

Table 2. Germination patterns among conidia of *Entomophthora muscae* discharged onto glass slips from house-fly cadavers during a 24-hour period at various relative humidities at 21°C.

Relative humidity	Percentages of forms present*						
	Primary alone	Primary with secondary	Secondary alone	Secondary with bulge	Secondaries germinating		Long germ tubes alone
					Germ tube short**	Germ tube long***	
100	27	29	24	0	7	16	7
94	22	21	13	7	37	0	0
85	17	14	29	27	13	0	0
75	16	3	47	23	11	0	0
65	29	8	51	5	7	0	0
55	33	5	43	8	11	0	0
48	41	4	52	1	2	0	0
38	24	11	61	4	0	0	0
6	48	18	33	1	0	0	0
0	73	17	9	1	0	0	0

* Average of four replicates, 100 forms per replication.
** Germ Tube Short = Length no greater than length of conidium.
*** Germ Tube Long = Length greater than length of conidium.

The foregoing results indicate that: 1, conidia falling through atmospheres with relative humidities ranging from zero to 100% do give rise to infections in flies (Table 1); and 2, long germ tubes, the invasive form of the fungus, are produced only at 100% R.H. (Table 2). When viewed together these findings suggest that the relative humidity within the boundary layer surrounding the fly's body is at or very near the saturation point. From an epizootiological viewpoint these findings also suggest that *E. muscae* can be transmitted within house-fly populations during periods of comparatively dry and cool weather. Low humidities in themselves do not prevent the spread of *E. muscae* infections in fly populations.

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Department of Entomology Cornell University Ithaca, New York 14853.

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STUDIES ON THE INCORPORATION OF [32 P]-PHOSPHATE
INTO LOW MOLECULAR WEIGHT RNA OF *DROSOPHILA*
MELANOGASTER CELL LINES

M. Matouschek, A. Dübendorfer and E. Kubli

Abstract.—In higher organisms the specific activity of the RNA obtained after feeding radioactive precursors to the animals is very low. Therefore, we have systematically studied the incorporation of [32 P]-phosphate into low molecular weight RNA of the following four *Drosophila melanogaster* cell lines: K_c, D₁, D₂, and line 3 of Schneider. After phenol-extraction the RNA was loaded on a 10% polyacrylamide gel. The tRNA region and the region between 4S and 5S (=tRNA "precursor" region) were eluted and the radioactivity measured in a liquid scintillation counter.

Three labeling procedures were used: 1) Addition of [32 P]-phosphate to the cell cultures in normal medium containing [31 P]-phosphate; 2) Culture of cells for one hour in phosphate-free medium before addition of [32 P]-phosphate; 3) Three hours without phosphates prior to the addition of [32 P]-phosphate. The [32 P]-phosphate pulse was two hours for all three types of experiments. The optimum incorporation was found with the cells of line 3 incubated under conditions 2.

The specific activities obtained were 108'000 cpm/A₂₆₀ for the RNA region and 9'700 cpm/A₂₆₀ for the "precursor" region. Modified nucleosides specific for tRNA were present in the region between 4S and 5S and also in the RNAs moving slower than 5S RNA on a 10% polyacrylamide gel. This suggests that tRNA precursors are localized in these regions. Schneider-3 cells were incubated for 2, 6, 12 and 24 hours with [32 P]-phosphate in order to determine the optimal incubation time for the labeling of stable tRNA. Twelve hours was found to give the highest specific activity of 670'000 cpm/A₂₆₀.

Introduction

The discovery that the primary transcription products of tRNA genes are precursor molecules larger than the tRNAs engaged in protein synthesis was originally made in mammalian cells (Burdon et al. 1967). It was shown that RNA of about 4.5S size could be converted into 4S molecules by crude cell extracts. At the same time these molecules acquired the nucleoside modifications characteristic for tRNAs. The detailed elucidation of the processing and nucleoside modifications leading to a mature tRNA were worked out in prokaryotes and most recently in lower eukaryotic cells (Altman 1978; Hopper et al. 1978; Knapp 1978). The major reasons for this success were the ease of selecting mutants, e.g. mutants blocking the processing steps

(Schedl and Primakoff 1973), the use of transducing phages (Altman and Smith 1971), and—for sequencing purposes—the high specific activities obtained after [^{32}P]-labeling.

Two major problems are encountered in studies of the primary transcription products of tRNA genes from higher organisms. Firstly, only low specific activities of the RNA are obtained by feeding or injecting radioactive precursors into animals. Secondly, the isolation and identification of specific tRNAs out of a mixture of many transcription products of about equal size is difficult. The first problem might be circumvented by the use of cell cultures, where higher specific activities can be obtained, the second problem by using organs synthesizing specific tRNAs in great amount, e.g., *Bombyx mori* silk glands (Garber et al. 1978), or isolation techniques able to pick up specific tRNA isoacceptors (Grosjean et al. 1973; Vögeli et al. 1975).

Drosophila melanogaster offers two advantages for studying the structure and function of tRNA genes in a higher organism: the possibility of localizing by “in situ”-hybridization genes that code for tRNAs (for a review see Kubli 1981) and sophisticated genetic techniques allowing the manipulation of the genome. Recently plasmids containing *Drosophila melanogaster* tRNA genes have been isolated and transcribed in *Xenopus laevis* oocyte nuclei (Schmidt et al. 1978). Precursor tRNAs of about 5S RNA size could be characterized. However, a careful comparison with products transcribed in the homologous “in vivo” system is still needed. The full nucleotide sequences of tRNA₁^{Met}, tRNA₁^{Lys}, and tRNA₂^{Phe} from *Drosophila melanogaster* have been determined by post-labeling techniques (Silverman et al. 1979a; Silverman et al. 1979b; Altwegg and Kubli 1979). The high degree of nucleoside modification found in tRNAs from eukaryotes sets some limits to these procedures. Conventional sequencing techniques (Brownlee 1972) using “in vivo” uniformly labeled [^{32}P]-tRNA are therefore still necessary to complement these recently developed elegant techniques. We have, therefore, decided to conduct a preliminary study on the incorporation of [^{32}P] into the low molecular weight RNA of four *Drosophila melanogaster* cell lines under various labeling conditions and to apply a specific affinity chromatography (Grosjean et al. 1973) for the isolation of a tRNA precursor.

Materials and Methods

Cell lines.—The following *Drosophila melanogaster* cell lines were used: K_c, D₁, D₂, and S (Schneider's line 3) (Schneider and Blumenthal 1978). The K_c cells were maintained in medium D₂₂ (Echalier and Ohanessian 1970), the other cell lines in the medium of Shields and Sang (1977) at 25°C in 30 cm³ Falcon flasks. The cells were subcultured after reaching a density of 10⁷ cells/ml. The cell lines D₁, D₂ and S were free of viruses whereas the line K_c contained DXV-viruses (Plus 1978).

Labeling procedures.—For the labeling experiments the cells were transferred into capped tubes on a roller drum or into spinner flasks, depending on the number of cells needed. Under these conditions the cells stayed in suspension and could be grown to a density of 15×10^6 cells/ml. Three procedures were used for the pulse-label experiments. 1.) Addition of [32 P]-phosphate to the cell cultures in normal medium containing [31 P]-phosphate. 2.) Culture of cells for 1 hour in phosphate-free medium before addition of [32 P]-phosphate. 3.) Three hours in phosphate-free medium prior to the addition of [32 P]-phosphate. The [32 P]-phosphate pulse was 2 hours for all three experiments.

RNA extraction.—The cells were lysed in 50 mM Tris-HCl, pH 7.5, containing 0.5% sodiumdodecylsulfate and 0.1% diethylpyrocarbonate at 0°C for 5 min.. The DNA was digested by addition of DNase (40 μ g/ml) at 0°C for 5 min. and the RNA subsequently extracted according to Kirby (1956). The high molecular weight RNA was removed by high-salt precipitation (Kern 1975), and the low molecular weight RNA in the supernatant was precipitated with ethanol. This RNA preparation was used for polyacrylamide gel electrophoresis and affinity chromatography. The aminoacyl-tRNA synthetases were prepared according to Twardzik et al. (1971) and the aminoacylation conditions were those of White and Tener (1973).

Polyacrylamide gel electrophoresis and affinity chromatography.—For the polyacrylamide gel electrophoresis the protocol of Fradin et al. (1975) was followed in detail. After autoradiography the RNA was eluted. The gel pieces were forced through the orifice of a 2 ml syringe and eluted over night at 37°C in 0.1 M Tris-HCl, pH 7.5, containing 0.5 M NaCl and 0.001 M EDTA. The gel particles were removed on a G-25 Sephadex column. After addition of rRNA as a carrier (40 μ g/probe) the RNA was ethanol precipitated. The procedure described by Grosjean et al. (1973) was used for the affinity chromatography.

Results

Pulse-labeling experiments.—Precursor tRNAs (ptRNAs) in *Bombyx mori* have been found on polyacrylamide gels to move between mature tRNA and 5S RNA (Garber et al. 1978). The gel region containing the mature tRNA was therefore studied separately from the region between mature tRNA and 5S RNA. This region will be referred to as "ptRNA" since it possibly contains tRNA precursors.

A comparison of the specific activities of the tRNA isolated from the four cell lines by the three different labeling procedures is shown in Figure 1a. The highest specific activity was obtained with S cells under labeling conditions 2. The low value for the D₂ cell line under these conditions may be an artifact. The lowest incorporation was measured with the K_c cells throughout all procedures.

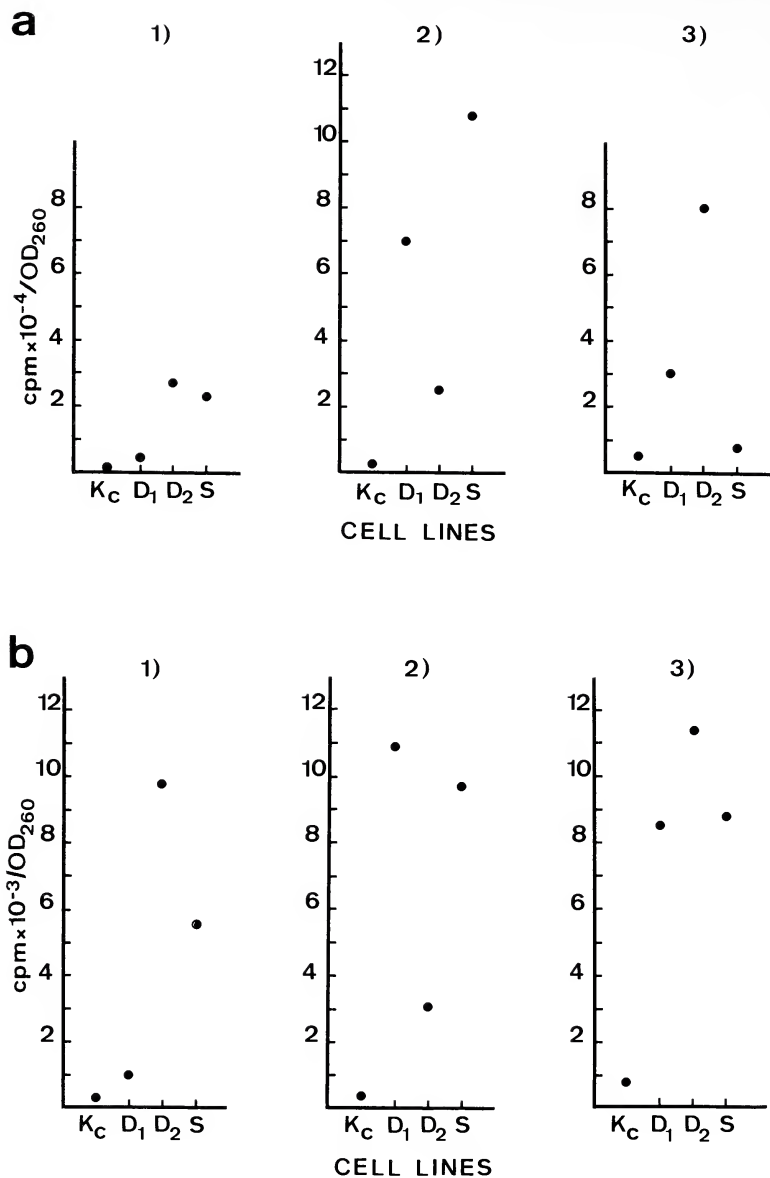


Fig. 1. a.) Specific activity of the RNA isolated from the tRNA region of a one-dimensional polyacrylamide gel under 3 labeling conditions: 1.) 0.1 ml monosodium [32 P]-phosphate (2.5 mCi; pH 5-6; NEX 063, NEN, Dreieichenhein, BRD) and 0.1 ml double concentrated medium was added to 4-9 ml cells in suspension (cell density $8-13 \times 10^6/\text{ml}$). 2.) 3.5-7 ml cell suspension ($15 \times 10^6/\text{ml}$) were centrifuged and washed with 3 ml medium without [31 P]-phosphate. The pellet was resuspended in the same medium to obtain a cell density of 15×10^6 cells/ml. The cells were kept in this medium for 1 hour on a roller drum (30 rev./min.). Then 0.1 ml

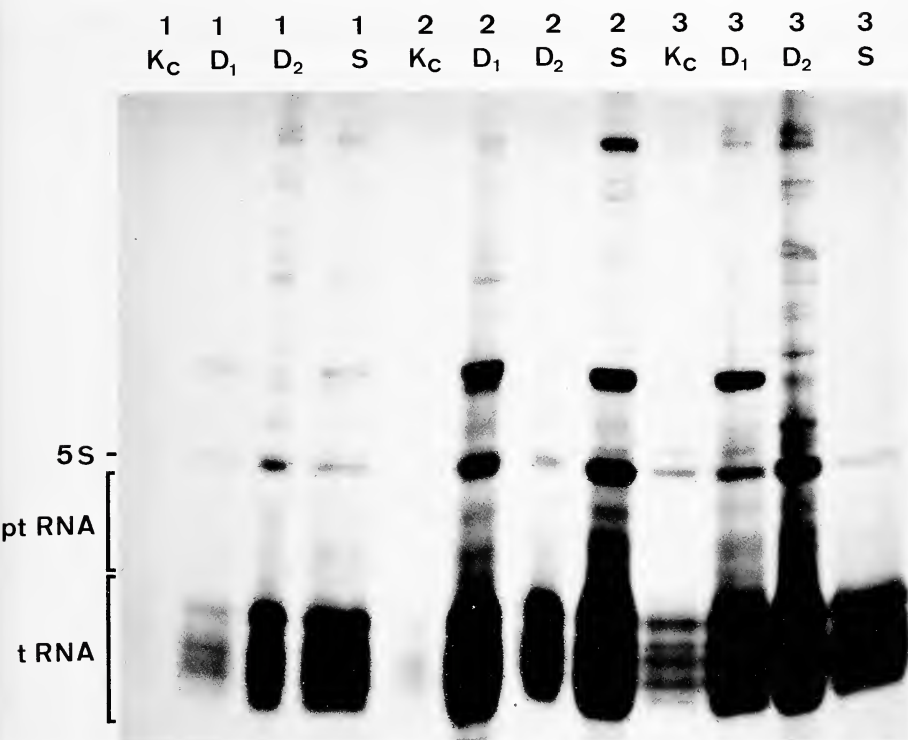


Fig. 2. One-dimensional polyacrylamide gel of RNA extracted from different cell lines labeled according to the protocol described in Figure 1a.

The specific activities of the “ptRNA” regions, though following a similar trend (Fig. 1b), were about an order of magnitude lower. Again the D₂ cells labeled under conditions 2.) showed reduced incorporation in comparison with the D₁ and S cells. Under these conditions the specific activity was slightly higher in D₁ cells than in S cells.

Polyacrylamide gel electrophoresis.—The results of the one-dimensional separation of the low molecular weight [³²P]-RNAs from the different cell lines are shown in Figure 2. No major differences in the pattern can be

←
monosodium [³²P]-phosphate and 0.1 ml double concentrated medium was added. 3.) Same as 2.) but incubation of the cells in [³¹P]-phosphate-free medium for 3 hours. After 2 hours of [³²P]-phosphate labeling the RNA was extracted and fractionated on a one-dimensional polyacrylamide gel. b.) Specific activity of the RNA isolated from the “ptRNA” region. Labeling conditions as described under a.).

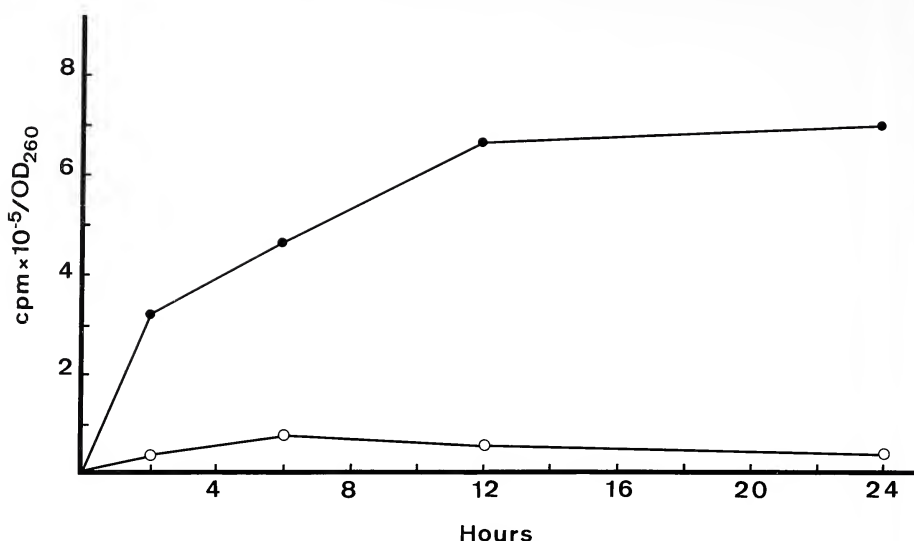


Fig. 3. Long term labeling of tRNA and "ptRNA." S cells were labeled under the conditions 2.) (see legend Fig. 1a) for 2, 6, 12 and 24 hours. The RNA was extracted and fractionated on a one-dimensional polyacrylamide gel. ●—● tRNA region, ○—○ "ptRNA" region.

detected in the "ptRNA" and tRNA regions. The RNAs moving slower than 5S RNA differ markedly in the different cell lines. However, the labeling procedure seems not to influence the labeling pattern.

Long term labeling experiments.—Considering the high incorporation values into the tRNA region obtained with the S cells we chose these for the long-term incorporation studies. Figure 3 shows that after 12 hours of labeling the specific activity levels off in the tRNA region. The maximal activity in the "ptRNA" region is already reached after 6 hours, but remains about an order of magnitude lower than the specific activity measured in the tRNA region.

Affinity chromatography.—The principle of the anticodon-anticodon affinity chromatography is based on the observation that some tRNAs with complementary anticodons can form a stable complex at low temperature (Eisinger 1971). A pure tRNA (e.g., tRNA^{Phe} of yeast or tRNA^{Glu} of *E. coli*) is covalently bound to a supporting material and poured into a column. In a mixture of tRNAs loaded on the column only those RNAs with the complementary anticodon form a stable complex at 4°C, the rest flows through. Increasing the temperature to 30°C and adding EDTA to the elution buffer destabilizes the complex: the formerly bound tRNA elutes as a single peak (Grosjean et al. 1973). Control experiments demonstrate that only the tRNA with the complementary anticodon is retained on the column, e.g., tRNA^{Phe} on a tRNA^{Glu} column (Fig. 4a). An example of an affinity chromatography

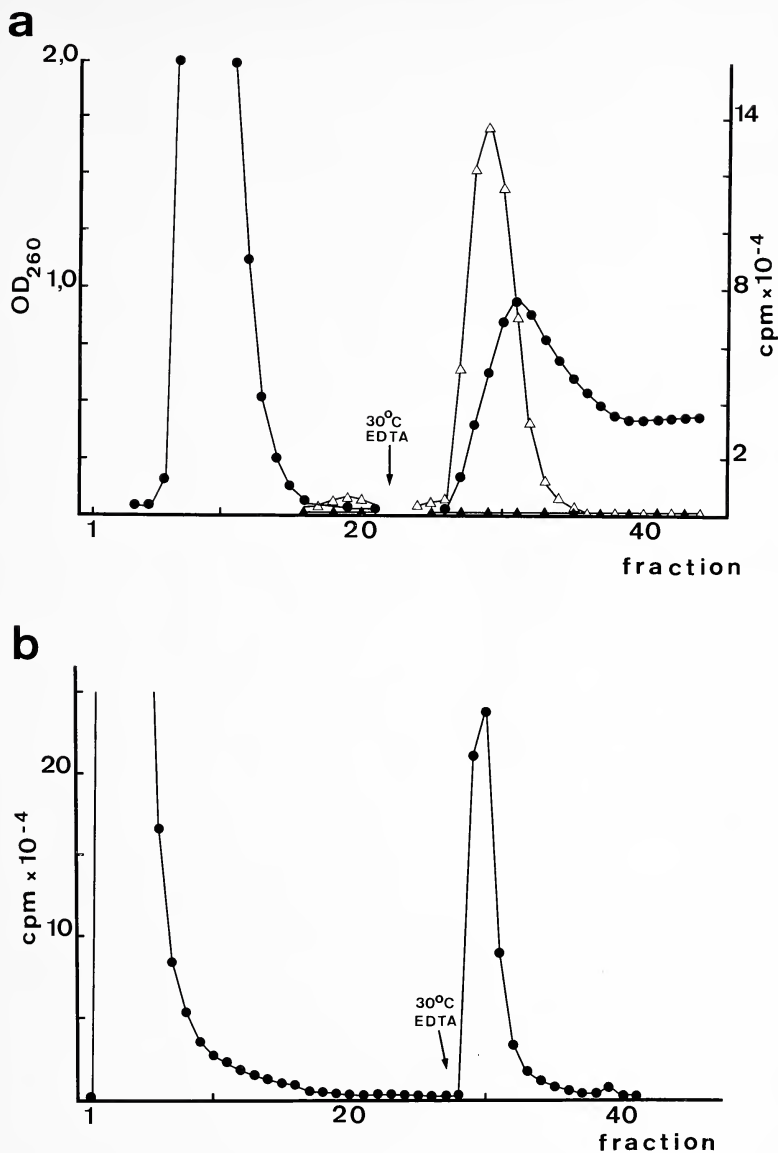


Fig. 4. a). $[^3H]$ -Phe-tRNA (\triangle — \triangle) and $[^{14}C]$ -Glu-tRNA (\blacktriangle — \blacktriangle) were cochromatographed on a tRNA^{Glu} affinity column. The $[^3H]$ -Phe-tRNA with the complementary anticodon is retained on the column and eluted at 30°C, the non-complementary $[^{14}C]$ -Glu-tRNA is eluted in the first peak. b). Affinity chromatography of $[^{32}P]$ -phosphate labeled tRNA on a tRNA^{Glu} column. The second peak contains $[^{32}P]$ -tRNA^{Phe}. Labeling conditions: 95×10^6 cells were labeled with 25 mCi $[^{32}P]$ according to conditions 2.) (see legend Fig. 1a) for 1 hour.

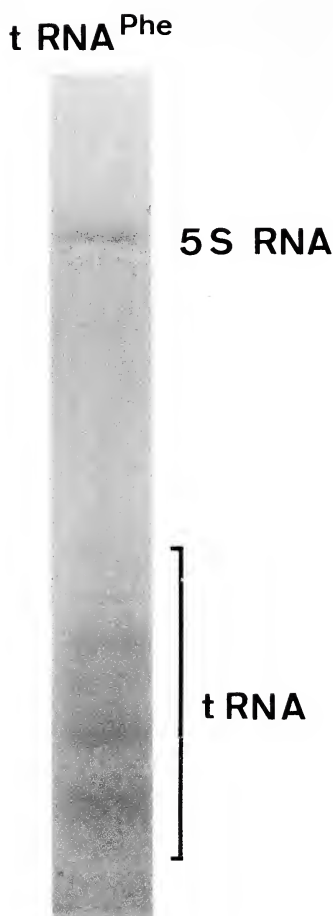


Fig. 5. One-dimensional polyacrylamide gel electrophoresis of [^{32}P]-phosphate labeled tRNA^{Phe} isolated by affinity chromatography (second peak Fig. 4b).

elution profile with pulse-labeled [^{32}P]-tRNA isolated from the S cell line is shown in Figure 4b. The second peak contains the tRNA^{Phe} with a complementary anticodon to the tRNA^{Glu} fixed on the column (Altwegg and Kubli, 1979). After precipitation this peak was loaded on a 10% polyacrylamide gel. The autoradiograph revealed about 8 bands in the tRNA region (Fig. 5). The bands were cut out and eluted. However, the radioactivity recovered was too low to allow a characterization of the different bands by fingerprinting. The identification was therefore not possible.

Discussion

The pulse labeling experiments show that the highest specific activity of the tRNA region is obtained with S cells under labeling conditions 2 (Fig. 1a). On the other hand, no similarly high specific activity is found in the "ptRNA" region of S cells. These seemingly contradictory results are understood in the light of the fact that some UV-absorbing material always co-elutes when the RNAs are eluted from the gels for measuring the specific activities. Considering the low concentration of RNAs in the ptRNA-region this UV-absorbing material creates a relatively high background that interferes with the calculation of the specific activity.

A comparison of the RNA pattern of the different cell lines on a one-dimensional polyacrylamide gel reveals that the tRNA regions do not differ considerably. However, major differences can be detected in the regions above 5S RNA (Fig. 2). This might reflect differential RNA extraction, but could also be due to the fact that some cell lines can be virus infected (Plus 1978) or aneuploid (Schneider and Blumenthal 1978). It has been reported that viruslike particles (VLP) of cultured *Drosophila melanogaster* cell lines contain a low molecular RNA which is believed to be the tRNA since this RNA can be aminoacylated (Shiba et al. 1980). However, the differences in the RNA patterns described here are not due to virus infections since the observed extra fractions of RNA all show up in the virus-free cell lines. On the other hand many cell lines do not contain a normal diploid set of chromosomes (Schneider and Blumenthal 1978), and since the tRNA genes are distributed over the entire *Drosophila* genome some tRNA genes might be missing and others increased in number. These problems have to be considered when tRNA preparations isolated from cell cultures are used for biochemical studies, such as the comparison of isoacceptor patterns, or the screening of plasmids containing tRNA genes. A further aspect deserving attention is the degree of modification of the tRNA isolated from cell cultures. For example, it has been shown that the tRNA^{His} and the tRNA^{Asn} isolated from *Drosophila melanogaster* cell cultures (S cells) do not contain the hypermodified base Q in the first position of their anticodon (Schmidt and Kubli 1980).

Affinity chromatography provides an elegant means of isolating tRNAs and their precursors (Grosjean et al. 1973; Vögeli et al. 1975). This method can only be used for the isolation of precursors if they do not contain insertion sequences near their anticodon. We obtained several bands upon separation of the second peak of the affinity column on a one-dimensional polyacrylamide gel (Fig. 5). This result can be interpreted in different ways, e.g., as unspecific binding to the tRNA hooked on the column, or as nuclease degradation of tRNA leaving the anticodon intact. Unfortunately the

activities obtained do not allow us to decide whether tRNA precursors were actually isolated. Pulse-label experiments with higher [^{32}P]-concentrations might give the necessary RNA activities to allow an adequate investigation of these problems.

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Institute of Zoology, University of Zurich, Switzerland.

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CONTINUOUS PRODUCTION OF PREDACIOUS MITES IN THE GREENHOUSE

R. M. Hendrickson, Jr.

Abstract.—The predacious mite species *Phytoseiulus persimilis* Athias-Henriot and *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae) were reared on potted red clover, *Trifolium pratense* L., in the greenhouse at ambient temperatures (min. 12°C). Twospotted spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae), were placed on the plants as prey. Red clover leaflets, on which were predators and prey, were removed and placed on potted alfalfa, *Medicago sativa* L., in the same greenhouse. One pot of red clover produced 5,000–8,000 predators per year, sufficient for satisfactory control of *T. urticae* on 50 pots of alfalfa. The technique requires minimal time, greenhouse space, and expense.

The purpose of this paper is to describe an unsophisticated technique for rearing predacious mites in a greenhouse used for arthropod research, with a minimum of time, space, and expense. The predators were used in routine biological control of twospotted spider mite, *Tetranychus urticae* Koch,^{1,2} on potted alfalfa in the same greenhouse.

Many excellent methods for rearing predacious mites have been published: for example, Ristich 1956; McMurtry and Scriven 1965; Kamburov 1966; and Gilstrap 1977. However, these techniques are relatively sophisticated and are most suitable for biological control workers specializing in the study of predacious mites. Burnett (1970a, b, 1971, 1977) has examined in detail the population relationships between the predacious mite *Amblyseius fallacis* (Garman) and *T. urticae* on alfalfa in greenhouse and field.

The primary reason for rearing alfalfa in the greenhouse was as a host plant for the introduced pest, the alfalfa blotch leafminer, *Agromyza frontella* (Rondani).³ (We reared 4 European parasite species on this host (Hendrickson and Barth 1979)). It was necessary to attempt biological control of *T. urticae* to avoid problems in insect rearing when alfalfa plants were treated with acaricides. Some common acaricides, at recommended dosages, were ineffective against *T. urticae*; others interfered with the rearing

¹ Acari: Tetranychidae.

² Determined by R. L. Smiley, R. J. Gagné, or P. M. Marsh, Systematic Entomology Laboratory, USDA-SEA-AR, % U.S. National Museum, Washington, DC 20560.

³ Diptera: Agromyzidae.

of *A. frontella*. For example, the effective acaricide oxythioquinox,^{4,5} apparently rendered alfalfa partially repellant to *A. frontella* for 3–4 weeks. As a result, sprayed plants produced ca. 10% of the number of *A. frontella* that untreated controls produced.

We reared the predacious mites *Phytoseiulus persimilis* Athias-Henriot⁶ and *Neoseiulus californicus* (McGregor)⁶ together on the same plants as an experiment in competitive displacement. Although *P. persimilis* has a proven reputation for effectiveness in greenhouses, it may not be the best predator under all greenhouse conditions. Since little has been published on the biological characteristics of *N. californicus*, we had no way to estimate its relative competitive ability vis-à-vis *P. persimilis* in the greenhouse. Oatman et al. (1977) showed that *P. persimilis* was more effective than *N. californicus* (= *Amblyseius californicus*) in field releases against *T. urticae* on strawberries. If the 2 species have the same ecological niche in the greenhouse, competitive displacement should take place. On the other hand, both species of predators may coexist based on exploitation of slightly differing ecological niches, with a net effect in the control of *T. urticae* superior to that of either predator species alone. Although preliminary results indicate that *P. persimilis* has rapidly increased in numbers relative to *N. californicus*, the experiment is incomplete and is not discussed further in this paper.

Prey culture.—The *T. urticae* culture was maintained in the laboratory at 22–28°C. We could not rear prey mites in the same greenhouse with predators because of the danger of contamination. Prey mites were placed on 3–5 day old snap bean seedlings, of which we planted 200 per week. The bean plants were grown to the 5-leaf stage and cut when mite populations had become abundant. One-half of the mite-infested cut bean plants were used to infest snap bean seedlings, and mites on the other half were used as prey for predators.

Predator culture.—Predators were maintained in the greenhouse on potted red clover plants, *Trifolium pratense* L. Red clover is a vigorous grower in the greenhouse even at low winter temperatures, withstands severe populations of *T. urticae* and frequent removal of foliage, produces leaflets of convenient size for production of predators, and is not a productive host for greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood)⁷.

⁴ Cyclic S,S-(6-methyl-2,3-quinoxalinediyl)dithiocarbonate.

⁵ This paper reports the results of research only. Mention of a pesticide in this paper does not constitute a recommendation for use by the U.S. Department of Agriculture nor does it imply registration under FIFRA as amended.

⁶ Acari: Phytoseiidae. Determined by H. A. Denmark, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville, FL 32602.

⁷ Homoptera: Aleyrodidae.

Prey-infested snap bean plants were cut at the 5-leaf stage and placed on predator-infested red clover plants. Foliage from 5–6 snap bean plants were placed on a single red clover plant each week. Occasionally a red clover plant was excessively infested with *T. urticae*, necessitating a recuperative period of 1–2 weeks during which no mites were placed on it.

Prey- and predator-infested red clover leaflets were trimmed from plants and placed on target alfalfa plants for *T. urticae* control. The older red clover leaflets, usually the most severely damaged by *T. urticae* feeding, sustained the highest populations of predators and the lowest populations of prey. Therefore, these leaves were preferentially removed.

To determine the approximate rate of predator production, we selected 40 leaflets at random and counted mite populations on them under the microscope. The numbers of predators (*P. persimilis* and *N. californicus* combined) per leaflet were: adults, 2.6 \bar{x} , 3.0 s; immatures, 4.0 \bar{x} , 4.3 s; and eggs, 3.1 \bar{x} , 3.8 s. The number of *T. urticae* per leaflet were: adults, 7.3 \bar{x} , 7.1 s; immatures, 44.4 \bar{x} , 59.4 s; and eggs, 73.2 \bar{x} , 99.7 s. Based on a count of the number of leaflets regularly removed from each pot, we calculate annual predator production (all stages) at 5,000–8,000 per pot of red clover.

How predators were used in the greenhouse.—We placed a predator and prey-infested red clover leaf, comprised of 3 leaflets, on each of 80–160 pots of alfalfa, which were used in insect rearing programs and which were cut back weekly to ca. 5 cm height. Thus, the actual numbers of predators and prey placed on each pot of alfalfa were 3 times the averages listed above. Cut-back plants may have carried predators from earlier inoculations, which would enhance the effect of newly added predators.

Predators were placed on potted alfalfa only once in each 5–10 week usage cycle unless problems developed with pesticides applied for control of greenhouse whitefly. (Attempts to use the parasite *Encarsia formosa* Gahan⁸ for *T. vaporariorum* control were unsuccessful because even parasitized immature whiteflies produced honeydew, which apparently rendered the plants unacceptable for oviposition by *A. frontella*.) We applied resmethrin^{5,9} at 2–3 week intervals in the warm seasons of the year for greenhouse whitefly control. Applications of resmethrin appeared to kill nearly all adult and immature predacious mites, but left predator eggs alive. Twospotted spider mites were unaffected by the pesticide, so that spotty outbreaks resulted. To prevent pesticide-induced upsets of *T. urticae*, we placed a single predator- and prey-infested red clover leaflet on each pot of

⁸ Hymenoptera: Aphelinidae. Kindly provided by M. J. Tauber, Dept. Entomology, Cornell Univ., Ithaca, NY.

⁹ [5-phenylmethyl]-3-furanyl)methyl *cis-trans*-(\pm)-2,2-dimethyl-3-(2-methyl-1-propenyl)cyclopropanecarboxylate.

alfalfa after the period of residual activity of resmethrin (3 days in warm seasons).

One pot of red clover provided enough predators for 50 pots of alfalfa. In general, the predacious mites gave us good control of *T. urticae*, better than previously attained with acaricides. The bench area required for 16 red clover plants in the greenhouse was 1.5 m².

On about one pot of alfalfa in 100, we observed *T. urticae* feeding damage on the first 15 cm of alfalfa regrowth, but at about this height, the predators built up sufficiently high populations so that the remaining alfalfa growth had no or very slight mite damage. Potted alfalfa used in rearing the alfalfa blotch leafminer was 35–50 cm in height, and mite damage on the bottom 15 cm was unimportant.

We estimated that 1½ h per week were required in this technique for successful biological control of *T. urticae* on 800 alfalfa plants. The time estimate includes planting beans, watering, movement of prey on bean leaves to red clover plants, and movement of prey and predators on red clover leaflets to alfalfa plants. The time spent was ca. 3 times that formerly required for the application of miticides, but was not excessive.

Discussion

The technique is useful for biological control of *T. urticae* in small greenhouses (ours is 100 m²). Its simplicity lends itself to routine application; it requires relatively little time, and only enough greenhouse bench space for one pot with predators per 50 pots with target prey; and it avoids complicating factors in research induced by acaricide applications.

The technique may have applicability in commercial greenhouses, since it is analogous to Gould et al. (1969) description of a 'banker' plant as a source for predacious mites in greenhouses used for cucumber production. In their concept, *T. urticae* on one cucumber plant in 100 was allowed to reach heavy population levels, then *P. persimilis* was added. As many as 5,000 predators were produced on a single cucumber plant for the remainder of the greenhouse. In the technique described in the present paper, prey and predators were introduced simultaneously on red clover 'banker' plants, with frequent addition of prey mites. The number of predacious mites produced (all stages), counted at the time of removal, was 5,000–8,000 per pot per year.

Other predators of *T. urticae* encountered in the greenhouse were *Anystis agilis* (Banks)^{2,10} and *Feltiella carolina* (Felt),^{2,11} but both species were un-

¹⁰ Acari: Anystidae.

¹¹ Diptera: Cecidomyiidae.

common and contributed little to control of *T. urticae*. Larvae of *F. carolina* fed on eggs and immotile forms of *T. urticae*. (A single individual of the parasite *Aphanogmus* sp.^{2,12} emerged from a puparium of *F. carolina*.)

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Beneficial Insects Research Laboratory, Agricultural Research, Science and Education Administration, USDA, 501 S. Chapel St., Newark, Delaware 19713.

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¹² Hymenoptera: Ceraphronidae.

CONSPECTUS OF PENTATOMINI GENERA OF THE WESTERN
HEMISPHERE—PART 2 (HEMIPTERA: PENTATOMIDAE)

L. H. Rolston and F. J. D. McDonald

Abstract.—A key is provided to separate the genera of Pentatomini of the Western Hemisphere that have a median tubercle or spine at the base of the abdominal venter which is unapposed apically by the posterior margin of the metasternum. New genera in this group are *Aleixus* McDonald, *Grazia* Rolston, *Kermana* Rolston and *Roferta* Rolston. One new species is described: *Aleixus virgatus* McDonald. New combinations are *Grazia tincta* (Distant, 1890), *Kermana bucera* (Stål, 1860), *K. imbuta* (Walker, 1867), *K. fucosa* (Berg, 1892) and *Roferta marginalis* (Herrich-Schäffer, 1836). A diagnosis is given for *Zorcadium* Bergroth, and *Z. truncatum* (Fallou, 1888) is redescribed.

In a preceding paper the tribe Pentatomini in the Western Hemisphere was divided into 3 sections. A key was provided for the genera of section 3, viz. those genera with a median tubercle at the base of the abdominal venter and with the metasternum produced ventrad in apposition to the apex of that tubercle (Rolston et al. 1980).

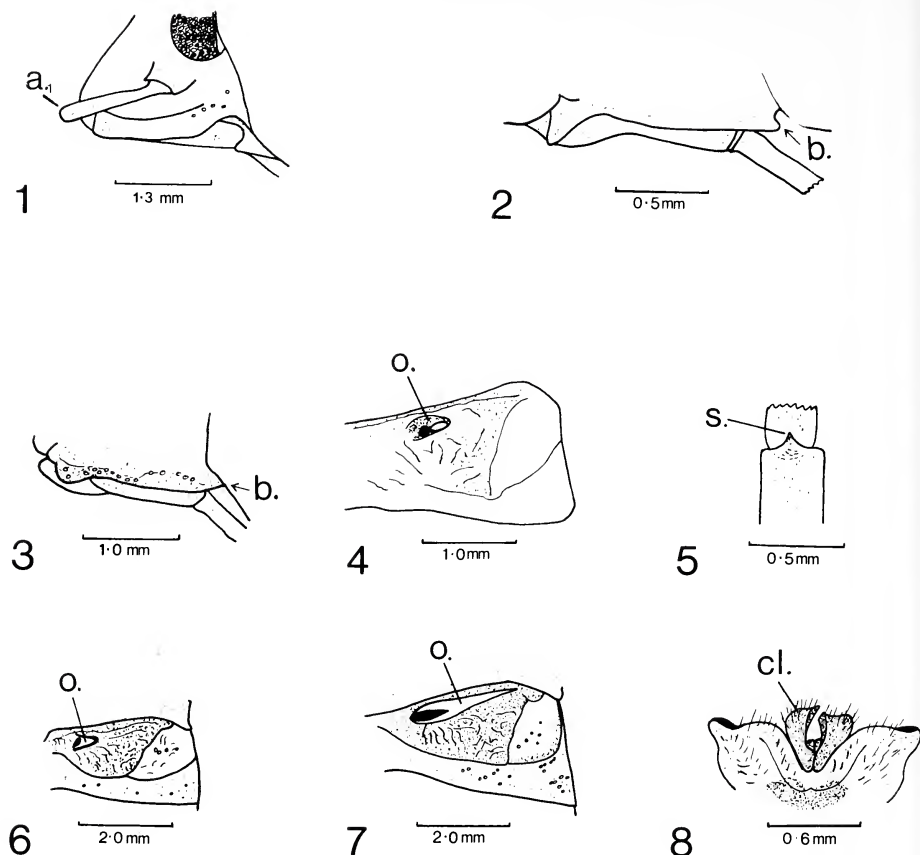
In this paper those genera are keyed that have a median tubercle or spine at the base of the abdominal venter but do not have the metasternum produced ventrad in apposition to the apex of that tubercle or spine. In fact, the abdominal spine often projects under the metasternum and may reach as far as the base of the head.

New genera added to this group are *Aleixus* McDonald, *Grazia* Rolston, *Kermana* Rolston and *Roferta* Rolston. *Aleixus* is monotypic, based on *A. virgatus* McDonald, n. sp. *Grazia* is also monotypic, based on *Piezodorus tinctus* Distant, 1890. *Kermana* contains 3 species, all previously named and in new combinations of *K. bucera* (Stål, 1860), *K. fucosa* (Berg, 1892) and *K. imbuta* (Walker, 1867), of which the last is type species. *Roferta* is monotypic, based on *Pentatoma marginale* Herrich-Schäffer, 1836.

The rare *Zorcadium truncatum* (Fallou, 1888) is redescribed and a diagnosis given for the monotypic genus. Since Fallou's type is missing a voucher specimen is designated.

Key to Genera of Pentatomini, Section 2

1. Stout pair of preapical spines present on inferior surface of posterior femora
Modicia Stål



Figs. 1-8. 1. *Ramosiana insignis*. Head, lateral view. 2. *Brepholoxa heidmanni*. Left buccula, lateral view. 3. *Nezara viridula*. Left buccula, lateral view. 4. *Brepholoxa heidmanni*. Left metathoracic stink gland orifice. 5. *Odmalea basalis*. Right fore femur, superior surface. 6. *Nezara viridula*. Left metathoracic stink gland orifice. 7. *Acrosternum hilare*. Left metathoracic stink gland orifice. 8. *Pellaea sticta*. Pygophore, caudal view, legend: antennal segment 1 (a.), buccula (b.), paramere (cl.), osteolar sulcus (o.), spine (s.).

- Femora not so armed 2
- 2. Median spine at base of abdominal venter projecting cephalad to procoxae *Disderia* Bergroth
- Median spine at base of abdominal venter not projecting as far cephalad as procoxae, sometimes reduced to tubercle 3
- 3. Distal end of first antennal segment clearly exceeding apex of head (Fig. 1) 4
- Distal end of first antennal segment not surpassing apex of head 5
- 4. Distal end of first rostral segment clearly surpassing bucculae; scutellar width at base about $\frac{2}{3}$ length *Ramosiana* Kormilev

- First rostral segment lying entirely between bucculae; scutellar width and length subequal *Vulsirea* Spinola
- 5. Bucculae lobed posteriorly from lateral view (Fig. 2) 6
- Bucculae evanescent posteriorly (Fig. 3) 12
- 6. Ostiolar canal extending less than halfway from inner margin of ostiole to lateral margin of metapleuron (Fig. 4); antennal segment 2 usually longer than or as long as each succeeding segment *Brepholoxa* Van Duzee
- Ostiolar canal extending more than halfway from inner margin of ostiole to lateral margin of metapleuron; antennal segment 2 shorter than each succeeding segment (except *Aleixus*) 7
- 7. Superior surface of femora prolonged distally as small spine (Fig. 5) 8
- Femora not so armed 11
- 8. Jugal contiguous before tylus 10
- Jugal usually separated apically, if contiguous then coria decidedly bicolored, stramineous and castaneous 9
- 9. Humeri bearing large dorsal tubercle (Fig. 10); second antennal segment longer than each succeeding segment *Aleixus* McDonald, n. gen.
- Humeri not tuberculate; second antennal segment shorter than each succeeding segment *Odmalea* Bergroth
- 10. Humeri cornute (Fig. 32); costal angle of coria extending caudad well beyond apex of scutellum *Zorcadium* Bergroth
- Humeri angulate or spinose; costal angle of coria extending caudad little if any farther than apex of scutellum *Thoreyella* Spinola
- 11. Median spine at base of abdominal venter projecting cephalad to or beyond anterior limit of mesocoxae; scutellum at least 1 tenth longer than basal width *Rio* Stål
- Abdominal spine shorter; scutellar width and length subequal *Dendrocoris* Bergroth
- 12. Ostiolar sulcus short, length about twice diameter of orifice (Fig. 6) 18
- Ostiolar sulcus reaching about halfway or more from inner margin of ostiole to lateral margin of metapleuron (Fig. 7) 13
- 13. Mesosternal carina compressed anteriorly, forming thin blade between procoxae *Piezodorus* Fieber
- Mesosternal carina nearly uniform in size and shape, sometimes obsolete on xyphus between mesocoxae 14
- 14. Superior surface of femora prolonged distally into small angulate tooth; parameres trilobed, posterior lobe curving mesoventrad and exposed in mesial depression in posterior margin of pygophore (Fig. 8). *Pellaea* Stål

- Femora unarmed; parameres simple or bilobed (Figs. 16, 22, 29), almost entirely concealed in genital cup 15
- 15. Lateral walls of genital cup bearing large tubercles near rim of cup (Figs. 21, 25, 28); scutellum strongly convex at least basally 17
- Tubercles on lateral walls of genital cup small or absent; scutellum weakly convex 16
- 16. Tibiae asculcate or weakly sulcate distally *Grazia* Rolston, new genus
- Tibiae clearly sulcate *Acrosternum* Fieber
- 17. Parameres with tubercle on cephalic margin between base and apex (Fig. 29); spermathecal bulb with 2 unequal diverticula (Fig. 31); median process at base of abdominal venter tuberculate *Roferta* Rolston, new genus
- Parameres with ventrolateral process (Fig. 22); spermathecal bulb bent into U (Fig. 24); abdominal spine projecting cephalad beyond metacoxae *Kermana* Rolston, new genus
- 18. Abdominal spine surpassing anterior limit of metacoxae; each spiracle on yellowish callus *Acrosternum abnorme* (Berg)
- Abdominal tubercle reaching only to posterior limit of metacoxae; spiracles unaccompanied by callus *Nezara viridula* (L.)

Aleixus McDonald, new genus

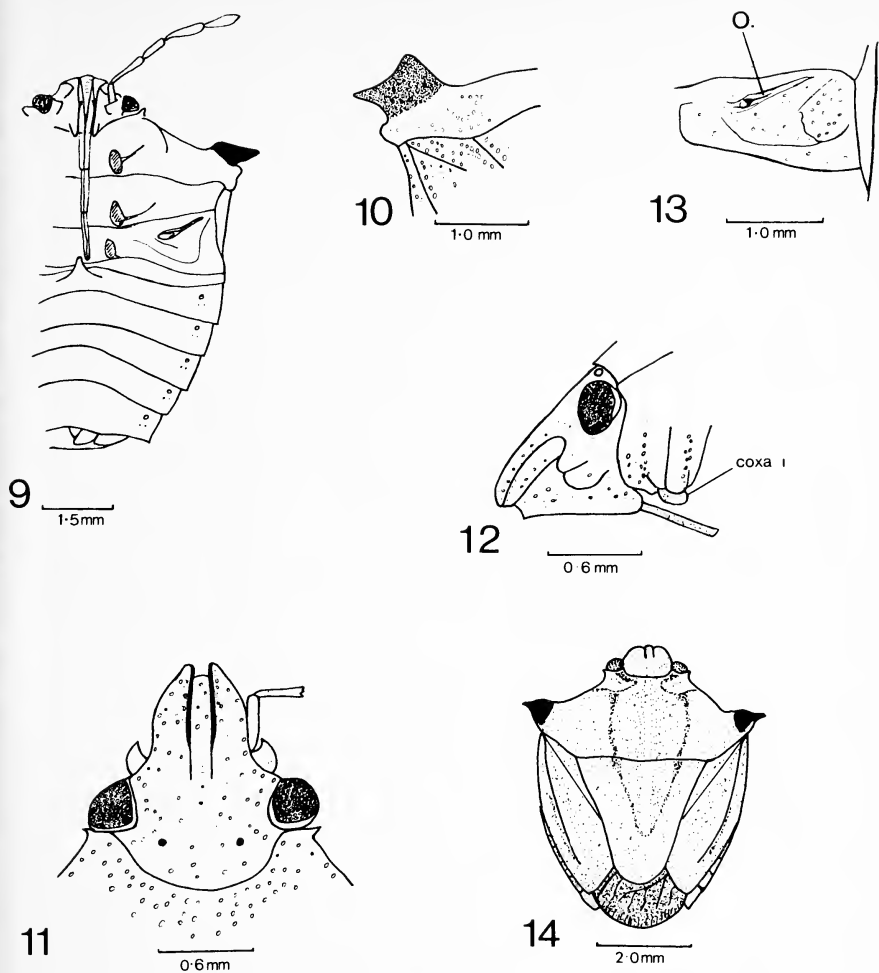
Type species.—*Aleixus virgatus* McDonald, n. sp.

Diagnosis.—Abdominal sternite 3 (second visible) with small median spine reaching metacoxae or nearly so (Fig. 9). Dorsal surface of each humerus bearing large tubercle (Fig. 10). Jugae narrowly rounded and separated apically, surpassing tylus (Fig. 11). First antennal segment not reaching apex of head; second segment longer than any other segment. First rostral segment lying entirely between bucculae, these projecting as lobes posteriorly onto prosternum (Fig. 12). Thoracic sterna nearly flat, not produced. Ostiolar sulcus extending about 6 tenths of distance from mesial margin of ostiole to lateral margin of metapleuron (Fig. 13). Superior surface of femora produced distally as small tooth, femora otherwise unarmed; tibiae sulcate; tarsi 3-segmented.

First gonocoxae lying mainly under sternite 7, visible only as small triangular sclerites.

Aleixus virgatus McDonald, n. sp.

Dorsal surface fulvid overlaid with dark brown punctation; tubercles on each humerus black. Dark brown stripe on each side of meson beginning at apex of pronotum, skirting cicatrice mesially, continuing onto scutellum, the 2 stripes converging about 3 quarters way down scutellum (Fig. 14); narrower brown stripes on each hemelytron, one along frenum, another



Figs. 9–14. *Aleixus virgatus*. 9. Ventral view. 10. Left humeral angle, dorsal view. 11. Head, dorsal view. 12. Buccula, lateral view. 13. Left metathoracic stink gland orifice. 14. Dorsal view, legend: osteolar sulcus (o.).

along radial vein. Membrane smoky brown. Venter amber overlaid with dark brown punctation. Length from apex of head to apex of abdomen 5.8 mm; width across humeri 4.5 mm.

Margins of jugae except mesial margin basally outlined in black (Fig. 11). Eyes rusty brown. Antennifers prominent. Antennal segments 1–3 reddish brown, slender; segment 4 reddish brown and slender basally, becoming paler and swollen apically; segment 5 amber, swollen; length of segments 0.31, 0.62, 0.43, 0.56, 0.50 mm. Rostrum reaching metacoxae (Fig. 9); basal

segment shorter than bucculae; segments 2-3 pale brown, segment 4 dark brown; length of segments 0.53, 0.77, 0.50, 0.43 mm. Width of head across eyes 1.45 mm, between eyes 0.8 mm; length of head 1.4 mm.

Pronotum steeply declivous anteriorly. Humeral angles produced into small knob; short cylindrical tubercle on dorsal surface of each humerus with distinct spine on lateral margin. Anterolateral margins of pronotum rounded dorsoventrally, entire; anterolateral angles projecting as small acute tooth. Pronotal length at meson 2.1 mm. Scutellum 2.9 mm wide at base, equally long; apex broadly rounded. Basal half of coria with reddish suffusion. Mesial impunctate line covering pronotum and scutellum.

Evaporative area on thorax granulose without fine rugae. Coxae, trochanters and femora yellow brown; tibiae and tarsi darker brown. Abdominal venter less heavily punctate than thorax.

Paratergites 8 medially fused. Paratergites 9 oblong, separated by second gonocoxae. Male unknown.

Holotype.—Female labeled "Km 8 Est. do Aleixo Manaus AM. BV. 26-VI-76. Nilu." Deposited in U.S. National Museum. Type no. 72138. No paratypes.

Grazia Rolston, new genus

Type species.—*Piezodorus tinctus* Distant, 1890.

Diagnosis.—Median spine on abdominal sternite 3 (second visible) projecting cephalad past mesocoxae, not attaining procoxae, largely obscuring metasternum, compressed, acute apically. Mesial carinae of mesosternum confined to anterior portion, weakly produced, widening near anterior mesosternal margin, not projecting onto prosternum. Ostiolar sulcus and ruga on each side reaching about 7 tenths of distance from mesial margin of ostiole to lateral margin of metapleuron. Femora unarmed; tibiae asulcate or very weakly sulcate, superior surface rounded. Bucculae little produced caudad of obtuse tooth, evanescent posteriorly; first rostral segment lying entirely between bucculae. First segment of antennae not reaching apex of head. Scutellum weakly convex basally.

Posterior surface of pygophore convex without median projection; genital cup of normal size, lateral walls without tubercle. Thecal appendages absent.

Comments.—This genus superficially resembles *Piezodorus* but differs in having a weak mesosternal carina, in lacking a median projection on the posterior pygophoral surface and in having the opening of the genital cup of normal size. The shape of the parameres and asulcate or very weakly sulcate tibiae distinguish *Grazia* from *Acrosternum*.

We are pleased to dedicate this genus to Dr. Jocélia Grazia of the Universidade Estadual de Campinas in recognition of her contributions to the taxonomy of neotropical pentatomids.

Since the holotype of *Piezodorus tinctus*, type species, is of limited value as a reference specimen by reason of being female and because some critical characters were destroyed in pinning, this species is redescribed from a series of 8 females and 4 males.

Grazia tincta (Distant, 1890) New Combination

Tan to light castaneous with brown to black and reddish markings. Reddish submarginal line on lateral border of juga and line on anterolateral margins of pronotum sometimes present. Fuscous to black markings often present but varying in frequency are: suture between juga (mandibular plates) and maxillary plates, thin line on lateral margin of juga, antennifers and first antennal segment laterally, antennal segments 2–4, few to many punctures plus surrounding areas on posterior disk of pronotum and base of coria, 2 or 4 macules at base of scutellum, small spot on disk of each corium and at distal end of each frenum. Black markings apparently present consistently are: posterolateral angles of sternites 3–7 and corresponding connexival angles, the latter mark sometimes extending partially or completely along posterior margin of each connexival segment.

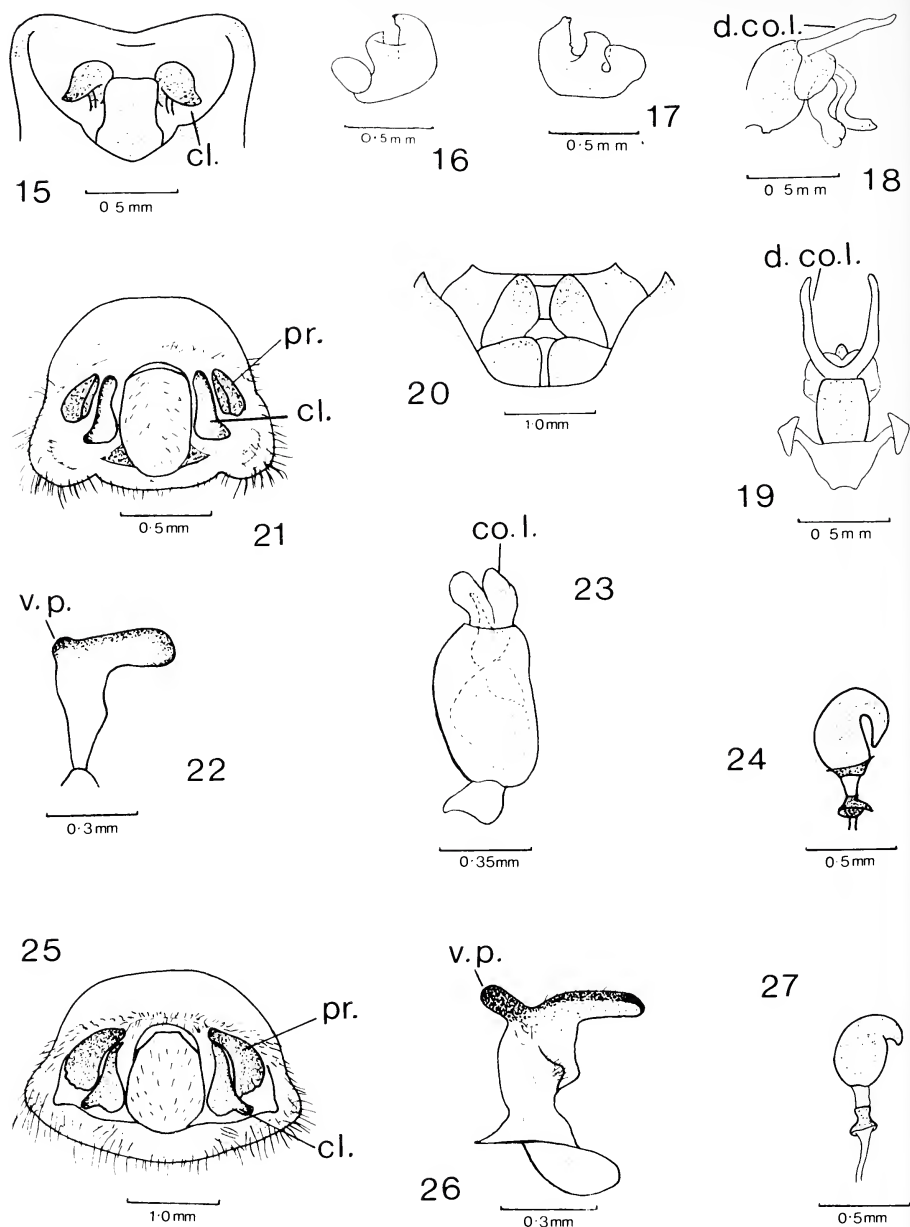
Dorsum of head flat; punctuation concolorous, rather fine and dense, arranged in subtle striae running anterolaterad from basal portion of tylus to lateral margin of juga and apparently randomly elsewhere. Lateral jugal margins sigmoid; apex of head moderately rounded; tylus a little longer than juga. Width across eyes 2.0–2.3 mm, length 1.6–2.0 mm; interocular distance 1.2–1.4 mm. Antennal segments 0.4–0.5, 0.45–0.5, 1.0–1.3, 1.15–1.5, 1.15–1.5 mm long. Rostral segments 2–4 about 0.9–1.1, 0.8–1.1, 0.7–0.8 mm long.

Pronotum more coarsely and sparsely punctate than head, punctuation usually a little stronger on posterior disk. Anterolateral margins straight. Humeral angles slightly produced, rounded, anterolateral and posterolateral margins forming right angle. Width at humeri 5.1–6.2 mm, length at meson 2.0–3.0 mm.

Scutellar apex narrowly rounded to subacute; punctuation similar to that on anterior pronotal disk; width at base 3.2–3.8 mm, length 3.6–4.5 mm; frena extending along basal 5–6 tenths of lateral margins. Coria shallowly and rather densely punctate, semitransparent, with posterolateral angle reaching from about middle of fifth to anterior part of sixth abdominal segments; membranes vitreous, their boundary with coria sinuous. Connexiva broadly exposed; posterolateral angle of each segment acutely produced.

Evaporative area matte, poorly defined. Abdominal venter tectiform, obtuse median ridge forming continuous profile with basal spine.

Posterior margin of pygophore moderately concave from both dorsal and caudoventral view. Head of parameres cupped, apical projection curving



Figs. 15-27. 15-20. *Grazia tincta*. 15. Pygophore, dorsal view. 16. Left paramere, outer view. 17. Left paramere, inner view. 18. Aedeagus, lateral view. 19. Aedeagus. 20. Female genitalia. 21-24. *Kermana imbuta*. 21. Pygophore, dorsal view. 22. Right paramere, outer view. 23. Aedeagus, lateral view. 24. Spermatheca. 25. *Kermana* sp. Pygophore, dorsal view. 26-27. *Kermana fucosa*. 26. Right paramere, outer view. 27. Spermatheca, legend: paramere (cl.), conjunctival lobe (co. l.), dorsal conjunctival lobe (d.co.l.), process of genital cup (pr.), ventral process of paramere (v.p.).

dorsolaterad and cephalad, obscuring small dorsolateral projection on rim of cup (Figs. 15, 16, 17). Conjunctiva with 3 pairs of lobes, each member of dorsal pair long, digitiform (Figs. 18, 19). Endophalic duct sigmoid from lateral view.

Genital plates as in Figure 20.

Distribution.—The 12 specimens seen came from the Dominican Republic, Panama, Venezuela, Ecuador, Brazil (Goias) and Paraguay.

Kermana Rolston, new genus

Type species.—*Rhaphigaster imbutus* Walker, 1867.

Diagnosis.—Median spine on abdominal sternite 3 projecting cephalad to mesocoxae. Basal half of scutellum strongly convex. First antennal segment not attaining apex of head. Bucculae evanescent at base of head; first rostral segment lying entirely between bucculae. Ostiolar ruga on each side extending about 6–8 tenths distance from mesial margin of ostiole to lateral margin of metapleuron. Mesosternum mildly tumescent on each side of meson; median carina weak, evanescent posteriorly. Metasternum not produced. Femora unarmed.

Genital cup bearing large process near rim on each lateral wall (Figs. 21, 25). Proctiger lacking tubercles. Ventrolateral process present on parameres, varying in size from knob to digit (Figs. 22, 26). Theca ovoid, lightly sclerotized. Conjunctiva entirely membranous, bilobed on each side, each lobe broadly rounded at apex (Fig. 23).

Spermathecal bulb wide at base, distally bent through 180 degrees (Figs. 24, 27).

Comment.—The most recent generic (or subgeneric) placement of the 3 species assigned to *Kermana* has been *Banasa* or *Acrosternum*. *Kermana* differs most notably from *Banasa* in having the abdominal spine projecting beneath the metasternum. In *Banasa* the metasternum slopes ventrad in an anterior to posterior direction and its posterior margin apposes the apex of the abdominal tubercle. *Kermana* differs especially from *Acrosternum* in possessing a large process on each lateral wall of the genital cup and in the much greater convexity of the scutellum.

The synonymy of the 3 species and a key for their separation follow.

Kermana bucera (Stål, 1860). New Combination

1860 *Rhaphigaster bucera* Stål, Sv. Vet. Akad. Handl. 2(7):23.

1872 *Banasa bucera*: Stål, Sv. Vet. Akad. Handl. 10(4):43.

1909 *Nezara (Banasa) bucera*: Kirkaldy, Cat. Hem. 1:122.

Kermana fucosa (Berg, 1892). New Combination

1892 *Nezara fucosa* Berg, Ann. Soc. Cient. Arg. 33:9.

1909 *Nezara (Acrosternum) fucosa*: Kirkaldy, Cat. Hem. 1:118.

1948 *Acrosternum fucosa*: Pirán, Acta Zool. Lill. 5:9.

Kermana imbuta (Walker, 1867). New Combination

1867 *Rhaphigaster imbuta* Walker, Cat. Het. 2:358.

1880 *Banasa imbuta*: Distant, Biol. Cent. Amer. Rhyn. 1:80, Pl. 7, fig. 10.

1909 *Nezara (Atomosira) imbuta*: Kirkaldy, Cat. Hem. 1:122.

1910 *Banasa imbuta*: Banks, Cat. Nearctic Hem.-Het.:83.

1916 *Banasa imbuta*: Van Duzee, Check List Hem. Amer.:8.

1917 *Banasa imbuta*: Van Duzee, Cat. Hem. N. Amer.:62.

Key to Species of *Kermana*

1. Humeral angles strongly produced laterad, narrowly rounded apically . . . (Brazil) *bucera* (Stål)
- Humeri scarcely produced 2
2. Punctuation and color of scutellum almost uniform; excised parameres somewhat Y-shaped with long ventrolateral process (Fig. 26) . . . (Argentina, Brazil, Uruguay) *fucosa* (Berg)
- Punctuation of scutellum weakest and most sparse in light colored areas at base and apex; excised parameres L-shaped with small ventrolateral process (Fig. 22) . . . (Texas to Costa Rica) *imbuta* (Walker)

Roferta Rolston, new genus

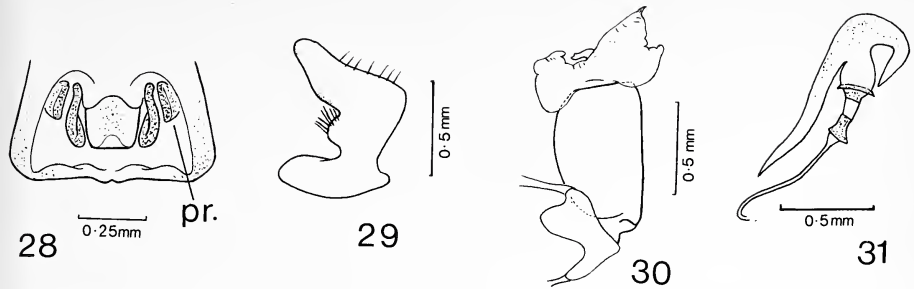
Type species.—*Pentatoma marginale* Herrich-Schäffer, 1836.

Diagnosis.—Median tubercle on abdominal sternite 3 short, obtuse, scarcely reaching metacoxae. Scutellum strongly convex. First antennal segment not attaining apex of head. Bucculae arcuate anteriorly, weakly produced caudad of arch, evanescent at base of head; first rostral segment lying entirely between bucculae. Ostiolar ruga on each side extending about 3 fourths of distance from mesial margin of ostiole to lateral margin of metapleuron. Mesosternum mildly tumescent on each side of meson; median carina moderately developed, extending full length of mesosternum. Metasternum similarly but less strongly carinate posteriorly. Femora unarmed.

Genital cup bearing large process on each lateral wall near rim (Fig. 28). Proctiger somewhat tuberculate subapically on each side. Parameres with tubercle on cephalic margin. Median penial plates and penisfilum short (Fig. 30).

Spermathecal bulb with 2 arms (Fig. 31).

Comment.—This genus is similar to *Kermana* but differs especially in the form of the parameres and spermathecal bulb. The type species, and only known member of the genus, is readily recognized by the dorsal color:

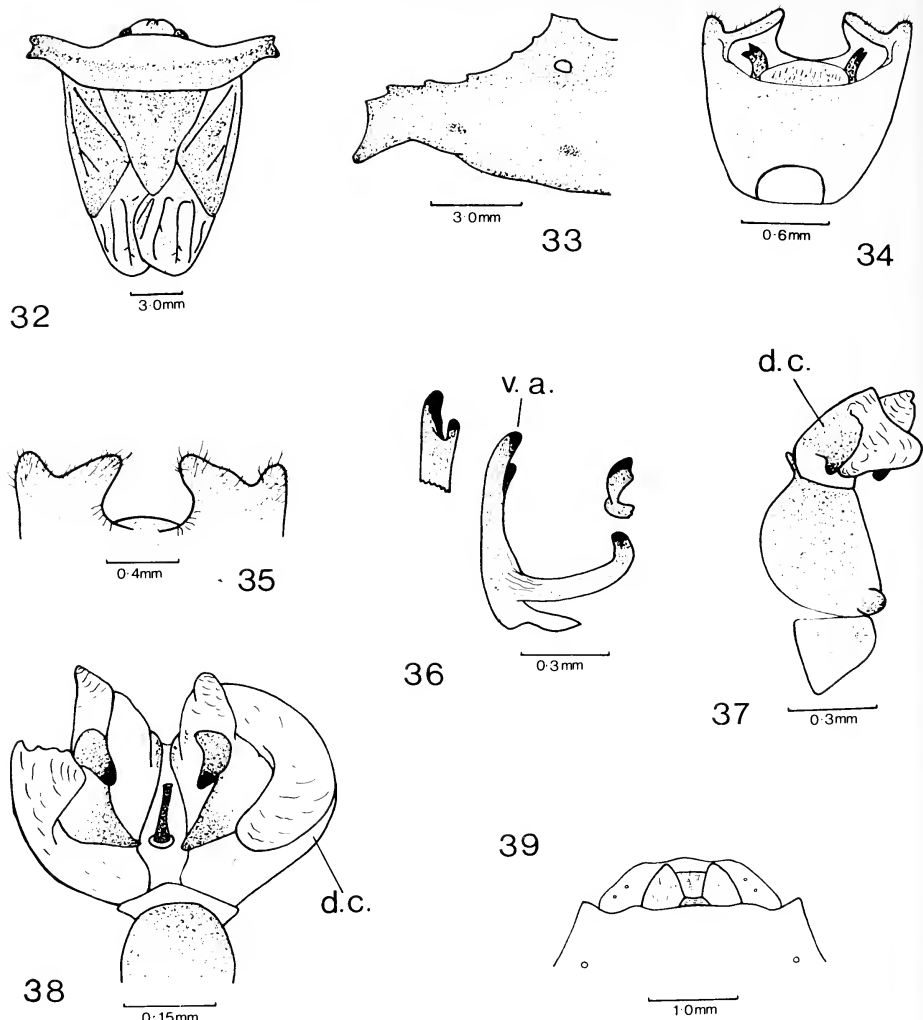


Figs. 28–31. *Rofertia marginalis*. 28. Pygophore, dorsal view. 29. Right paramere, mesial face. 30. Aedeagus, lateral view. 31. Spermatheca, legend: process of genital cup (pr.).

fuscous with a broad orange-yellow border around the body (but not the head) and median stripe of the same color on the pronotum and scutellum. The synonymy of the species follow.

Roferta marginalis (Herrich-Schäffer, 1836) New Combination

- 1836 *Pentatoma marginale* Herrich-Schäffer, Wanz. Ins. 3:59, fig. 320.
 1837 *Pentatoma nitida* Westwood, Cat. Hope 1:33–34 (synonymized by Dallas, 1851, & Distant, 1900a).
 1845 *Rhaphigaster marginalis*: Herrich-Schäffer, Wanz. Ins. 8:16.
 1851 *Rhaphigaster marginalis*: Dallas, List Hem. 1:281.
 1861 *Ptilarmus marginalis*: Stål, Stett. Ent. Zeit. 22:141.
 1867 *Strachia olivacea* Walker, Cat. Het. 2:322 (synonymized by Distant, 1900a).
 1867 *Rhaphigaster marginalis*: Walker, Cat. Het. 2:359.
 1868 *Strachia marginalis*: Walker, Cat. Het. 3:561 (not 2:343–344).
 1872 *Nezara marginalis*: Stål, Sv. Vet. Ak. Handl. 10(4):40.
 1892 *Nezara marginalis*: Berg, Anal. Soc. Cient. Arg. 33:6.
 1893 *Arocera olivacea*: Lethierry & Severin, Cat. Hem. 1:159.
 1893 *Nezara marginalis*: Lethierry & Severin, Cat. Hem. 1:166.
 1900a *Nezara marginalis*: Distant, Ann. Mag. Nat. Hist. (7)5:392.
 1900b *Nezara marginalis*: Distant, Proc. Zool. Soc. London: 823.
 1909 *Nezara (Nezara) nitida*: Kirkaldy, Cat. Hem. 1:116.
 1910 *Nezara marginale*: Valdés, Anal. Acad. Cien. Méd., Fis. y Nat. Habana, Cuba. 46:429 (laps. cal.).
 1932 *Nezara nitida*: Barber & Bruner, J. Dept. Agr. Puerto Rico 16(3):262–263.
 1935 *Acrosternum nitida*: Fennah, Trop. Agr. Trinidad 12:193.
 1946 *Acrosternum marginale*: Barber & Bruner, Brooklyn Entomol. Soc. 40(2):52–53.



Figs. 32-39. *Zorcadium truncatum*. 32. Dorsal view. 33. Humeral angle of pronotum, dorsal view. 34. Pygophore, dorsal view. 35. Pygophore, ventral border. 36. Right paramere, lateral view; apices, dorsal view. 37. Aedeagus, lateral view. 38. Aedeagus, ventral view. 39. Female genitalia, legend: dorsal conjunctival appendage (d.c.), ventral arm of paramere (v.a.).

1948 *Acrosternum nitida*: Callan, Proc. R. Entomol. Soc. London (B) 17 (9/10):117.

1949 *Acrosternum elegans* Bruner & Barber, Mem. Soc. Cubana Hist. Nat. 19:160-161. NEW SYNONYMY.

1967 *Acrosternum elegans*: Alayo, Mus. Felipe Poey Trab. Divul. 43:27, 28, Pl. 5, fig. 3.

1976 *Acrosternum nitidum*: Rolston, J. N.Y. Entomol. Soc. 84(1):3.

The syntypes of *Pentatoma nitida* Westwood, one syntype of *Strachia olivacea* Walker (the second syntype was not located) and the holotype of *Acrosternum elegans* Bruner & Barber were examined. These specimens appear to be conspecific.

Barber and Bruner (1946) noted that Kirkaldy (1909) apparently erred in rejecting *Pentatoma marginale* Herrich-Schäffer, 1936, as preoccupied. I have not found a prior usage of this name.

Zorcadium Bergroth, 1918

Zorcadium Bergroth, 1918, Ann. Mus. Natl. Hung. 16:307–308.

Type species.—*Euschistus truncatus* Fallou, 1888, by monotypy.

Diagnosis.—Median abdominal spine on sternite 3 stout, reaching mesocoxae. Humeral angles greatly produced, cornute, much elevated (Fig. 33). Prosternum essentially flat; mesosternum slightly tumescent on each side of meson, without carina; metasternum flat, not produced. Bucculae prolonged as lobe at base of head, surpassing distal end of first rostral segment; apex of rostrum reaching mesocoxae. Femora armed only by distal extension of superior surface into small acute spine. Ostiolar canal long, curved. Jugal contiguous before tylus. First segment of antennae not reaching apex of head, subequal in length to segment 2, half or less length of each of last 3 segments. Costal angle of coria extending well past apex of scutellum.

Zorcadium truncatum (Fallou, 1888)

Euschistus truncatus Fallou, 1888, Naturaliste p. 36.

Zorcadium truncatum: Bergroth, 1918, Ann. Mus. Natl. Hung. 16:308 (re-description)

Yellowish brown base color; irregularly punctate with dark castaneous to black, rather thickly so on dorsum (Fig. 32).

Head a little wider than long, 2.2 mm across eyes; 2.0 mm long. Lateral margins of jugal curving sinuously to narrowly rounded apex. Punctuation somewhat clustered on each side of tylus toward base, in part arranged in irregular longitudinal lines on each side of vertex. Distance between eyes 1.4 mm, across ocelli 1.2 mm. Antenniferous tubercles largely exposed from above; length of antennal segments 0.5, 0.5, 1.1, 1.1, 1.3 mm.

Pronotum 8.3 mm wide across humeri, 2.5 mm long at meson. Anterolateral angles produced into small tooth; anterolateral margin obtuse with scattered black denticles. Humeral angles distally curving posteriorly with posterolateral angle farther produced as subacute spine (Fig. 33). Anterior pronotal disk strongly deflexed, calloused and impunctate mesially, behind cicatrices subcalloused and somewhat sparsely castaneously punctate excepting 4 clusters of punctures arranged equidistantly in a nearly transverse

line; each cicatrice with large pale callus near middle; punctation in and surrounding cicatrices mostly fuscous to black; punctation dense along front portion of posterior disk.

Scutellum 3.8 mm wide at base, 3.4 mm long, with a pale subcalloused basal spot near each angle; punctation sparse along midline; distal end of each frenum marked by fuscous spot; lateral margins convex along frena, beyond frena parabolic with narrowly rounded apex. Punctation of coria finer than on scutellum, lacking in lacuna near distal end of radial vein. Membrane of hemelytra fuscous; veins few, darker, simple with occasional spur. Connexivum narrowly exposed, finely punctate, a few punctures at sutures black, others brown.

Evaporative areas sparsely and finely black punctate. Venter of head, thorax and abdomen on sternites 2–4 between spiracular line and middle of disk rather coarsely punctate; abdomen more finely punctate laterad of spiracular line, nearly impunctate and with broad dark streak down middle of abdominal disk. Spiracles concolorous with surrounding part of sternites.

Ventral margin of pygophore with deep median U-shaped emargination (Fig. 35), border developed into two distinct flattened lobes on each side of emargination (Fig. 34); dorsal margin broadly arched. Proctiger box shaped, flat dorsally, free margins narrow and vertical. Claspers C-shaped, compressed; ventral arm longest, bifid, forming 2 short heavily pigmented blunt fingers; dorsal arm short, concealed under dorsal margin of pygophore, apically blunt and heavily pigmented (Fig. 36).

Theca oval, produced apically into narrow rim bearing pair of rounded lobes dorsally. Dorsal conjunctival appendages forming large lightly sclerotized shield surrounding ventral conjunctival appendages and endophalic duct; shield produced laterally into flap on each side (Fig. 37); ventral conjunctival appendages when not expanded enclosed by dorsal appendages, bifid, forming 2 heavily pigmented horns, the ventral horn larger (Fig. 38). Endophalic duct short, almost straight, projecting centrally at base of conjunctiva. Median penial lobes absent.

Basal plates of female concealed; tenth sternite subquadrate (Fig. 39).

Voucher specimen.—Female labeled (a) "Forested eastern foothills of the Andes, 2000 ft." (b) "Peru: Tingo Maria 1 km E. of town. At edge of woodland, 5. viii. 1971." In the British Museum (Natural History).

Comment.—The holotype of *Euschistus truncatus* was in the Museum National d'Histoire Naturelle, Paris, but has been misplaced or lost according to Prof. J. Carayon (personal communication). In addition to the voucher specimen, a male is in the private collection of Dr. H. Dodge Engleman.

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Dr. P. Alayo's help was indispensable in solving the mystery of Valdés' listing of *Nezara marginale*.

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(LHR) Department of Entomology, Louisiana State University, Louisiana Agricultural Experiment Station, Baton Rouge, Louisiana 70803 and (FJDM) Department of Plant Pathology and Agricultural Entomology, University of Sydney, Sydney, N.S.W. Australia 2006.

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2. Key to genera of Pentatomini, Section 3. pp. 121–123.
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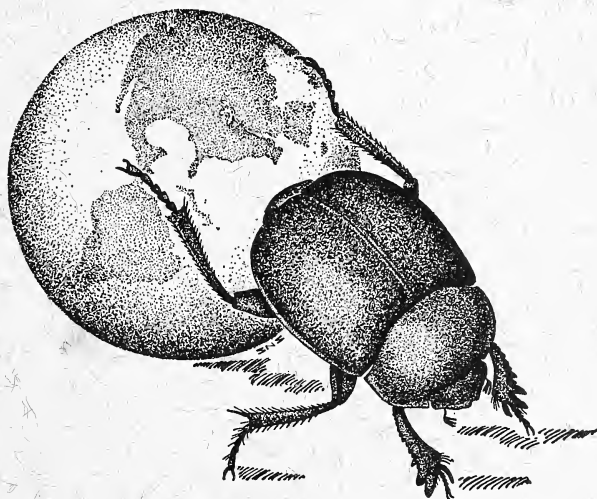
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THE OCCURRENCE AND RELEVANCE OF ARTHROPODS OF MEDICAL AND VETERINARY IMPORTANCE CAPTURED DURING A SURVEY ON PLUM ISLAND, NEW YORK

Dennis J. White and Cherylann P. White

Abstract.—Since 1954, the United States Department of Agriculture has maintained a high containment biological research laboratory on Plum Island, New York, involved with research and diagnoses of exotic communicable animal diseases. Isolation from the Long Island mainland provides a physical barrier to foreign disease transmission to mainland livestock and of domestic animal diseases to Plum Island livestock. At the request of the Plum Island Animal Disease Center administration, this survey was conducted to define the entomological fauna of medical and veterinary importance and to determine potential vectors of both native and migrating species. In addition to the insect survey, mosquito pools were used for native virus isolation attempts, sera from mammalian and avian specimens were used for detection of antibodies to arboviruses and engorged mosquitoes were used for blood meal identification.

Twenty native culicid and fifteen tabanid species predominated in the collections in addition to at least three species of migrants from the Orient Point, New York salt marshes. All mosquito pools and avian sera were negative when screened for CEV, EEE, SLE, WEE and POW viruses or antibodies. Two mammalian sera reacted by HI to California and St. Louis encephalitis viruses at low titers. Mosquito blood meal analyses showed an avian host preference for the *Culiseta* species and a rodent host preference for the *Aedes* species.

Introduction

The United States Department of Agriculture animal disease research facility (Anonymous 1975) has been located on Plum Island since 1954. The center is engaged in both basic and applied research on exotic communicable diseases of animals and is the only facility in the United States so designated. In addition to educational and technical services provided to United States and foreign governments, the Plum Island Animal Disease Center's (PIADC) responsibilities are threefold: develop diagnostic capability of exotic animal diseases, conduct basic and applied research on these diseases and their causative organisms, and develop procedures for safe importation of foreign wild and domestic animals, semen, meat and other animal products. The central objective of the facility is to assist in the prevention of the

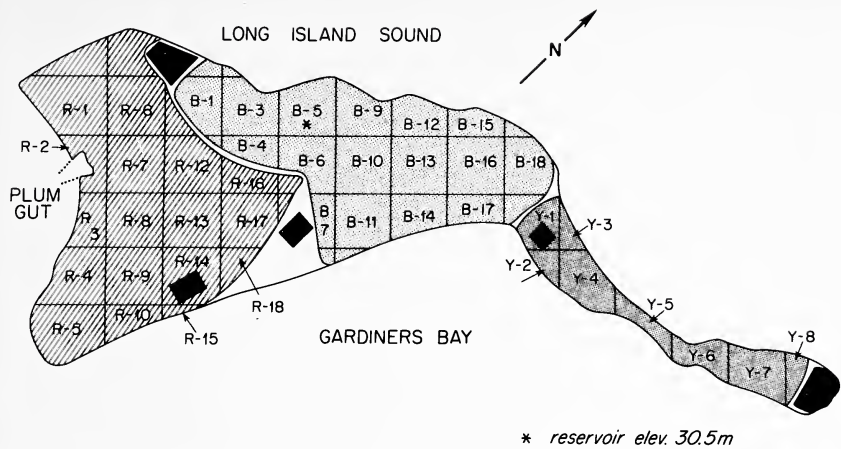


Fig. 1. Habitat differentiation and quadrant delineation for Plum Island survey. R = old estuarine and predominant lentic vegetation; B = dominant upland vegetation; Y = coastal and upland vegetation in close proximity.

introduction of animal disease that could result in death or serious economic losses in susceptible livestock populations in the United States.

Due to security measures necessary for P3 level biological containment, rigid safety regulations have been established. All movement to, from and on the island is strictly monitored to eliminate all chances of unintentional transmission of microorganisms or contaminated material. In order to enhance biological containment, Congress stipulated that the Center be located on an island entirely under Federal control and surrounded by deep navigable water so as to provide a physical barrier for transmission of foreign diseases from Plum Island to the mainland and domestic diseases from the mainland to Plum Island. Plum Island is located 2.1 km from the eastern tip of Long Island's north fork and covers 320 ha. At its widest, the island is 1.6 km wide, which tapers to 0.1 km at the narrowest part and is 4.3 km long (Fig. 1).

The announcement of a proposal to study Rift Valley Fever, a mosquito-borne disease presently epidemic in Africa, prompted local public officials to visit the facility. In December 1978, New York State Department of Health officials toured the PIADC. During the course of this visit, State Health Department officials were invited to conduct an entomological survey of the island. The purpose of this report is to define the entomological fauna native to, or captured on, Plum Island that is of medical or veterinary significance and present the results of a basic arbovirus survey.



Fig. 2. Topographic map of Plum Island.

Materials and Methods

Licenses were received from the United States Department of the Interior, Fish and Wildlife Service for avian collection and from the New York State Department of Environmental Conservation for mammal collection. The survey began on 21 May 1979 and terminated 25 September 1979. Prior to specimen collection, maps were drawn on a grid system to readily provide locality descriptions and habitat definitions.

The island was divided into 3 sections (Fig. 1) based on predominant topographical features (Fig. 2). The R sector, ca. 150 ha, is distinguishable by the predominant old estuarine and lentic vegetation associated with lower elevations (Table 1). The B sector, ca. 130 ha, is characterized by deciduous vegetation associated with higher elevations. The Y sector, ca. 40 ha, included the eastern peninsula and is characterized by upland and coastal vegetation in close proximity.

Diverse collection techniques were employed. Phototropic mosquitoes were collected by 2 permanent New Jersey light traps and four portable CDC light traps. Resting boxes were distributed throughout the island. A malaise trap was placed in an area where tabanids were abundant. Ixodid ticks were captured by dragging a 1 m² piece of white flannel cloth along

Table 1. Dominant vegetation found in each of the three major habitats on Plum Island.

R-Sector

Baccharis halimifolia L.—Groundsel bush
Iva oraria (Bartlett)—Marsh elder
Hibiscus palustris (L.)—Rose mallow
Phragmites communis Trin.—Ditch reed
Rhus radicans L.—Poison ivy
Myrica pensylvanica Loisel—Bayberry
Rhus copallinum L.—Shining sumac
Pinus resinosa Ait.—Red pine
Chamaecyparis thyoides (L.)—Atlantic white cedar
Ammophila breviligulata Fern.—Dune grass
Typha angustifolia L.—Cattail

B-Sector

Quercus velutina Lam.—Black oak
Quercus coccinea Muenchh.—Scarlet oak
Quercus palustris Muenchh.—Pin oak
Acer platanoides L.—Norway maple
Salix babylonica L.—Weeping willow
Populus tremuloides Michx.—Quaking aspen
Populus alba L.—White poplar
Nyssa sylvatica Marsh—Black tupelo
Prunus serotina Ehrh.—Black cherry
Sassafras albidum (Nutt.)—Sassafras
Rhus copallinum L.—Shining sumac
Rhus typhina L.—Staghorn sumac
Rhus radicans L.—Poison ivy
Lonicera japonica Thunb.—Honeysuckle
Myrica pensylvanica Loisel—Bayberry
Rubus cuneifolius Pursh.—Blackberry

Y-Sector

Rosa virginiana Mill.—Wild rose
Phragmites communis Trin.—Ditch reed
Rhus radicans L.—Poison ivy
Myrica pensylvanica Loisel—Bayberry family
Rhus copallinum L.—Shining sumac
Rhus typhina L.—Staghorn sumac
Rubus cuneifolius Pursh.—Blackberry
Quercus velutina Lam.—Black oak
Quercus coccinea Muenchh.—Scarlet oak
Quercus palustris Muenchh.—Pin oak
Prunus serotina Ehrh.—Black cherry
Ammophila breviligulata Fern.—Dune grass
Chamaecyparis thyoides (L.)—Atlantic white cedar

vegetation. Attempts to locate argasid ticks were done by sifting sand surrounding seagull nests (H. Hoogstraal, NAMRU-3, Cairo, Egypt, personal communication). Immature mosquitoes were collected by dipping. Sweep nets were used to capture blood seeking specimens of mosquitoes, deer flies, horse flies, stable flies and other filth-breeding muscids. Biting species too small to be retained in a sweep net (e.g. *Culicoides*) were collected only as they were feeding. Active ectoparasites (ticks, fleas, lice, etc.) were removed from hosts captured in Hav-a-hart mammal traps or avian mist nets.

In addition to the arthropod specimens, 0.1 to 0.9 cc of blood was drawn from each of the captured mammals and birds to detect presence of antibody to arboviruses. Giemsa-stained blood smears of 23 mammals were made for detection of protozoal parasites (i.e. *Babesia microti*). The hemolymph test (Burgdorfer 1970) was performed on 80 captured *Dermacentor variabilis* (Say). Arbovirus isolation attempts using suckling mice were made from frozen pools of mosquitoes collected in CDC traps. Engorged mosquitoes captured by any method were used for blood meal identification using the capillary-precipitin technique (Edman 1971). Thirty-five avian and 23 mammalian sera were tested by hemagglutination-inhibition tests (Clark and Casals 1958).

Selected specimens of all invertebrates collected have been presented to the PIADC for reference purposes.

Results

Island topography.—The island ranges in elevation from 0 to 30.5 m above sea level (Fig. 2) and is surrounded by a rocky-sandy beach ca. 10–20 m wide at high tide. A once existent salt marsh at the extreme southwest part of the island had been diked to prevent tidal inundation. Routine water analyses performed by the PIADC staff confirmed our observations that no collections of salt or brackish water are present on the island. Three major fresh water swamps cover ca. 50 ha in the western half of the island and a few small fresh water ponds are scattered over the island. The sandy nature of the island allows quick percolation or run off of rain water from the surface. The upland areas are densely covered with scrub vegetation (Table 1).

Arthropod specimens.—A summary of all captured specimens is included in Table 2. Twenty-two species of mosquitoes were collected during the study, 8 as larvae and 19 as adults. Ten species were collected from the fresh water swamp group, only 4 of which were captured as immatures. The relatively large proportion of specimens of this group (74.5% of adult mosquitoes) illustrates the extent of breeding that occurred in these swamps. Most of these species were captured in CDC light traps.

Many discarded tires used around a sewage settling pond in the R-6 quad-

Table 2. Number and location of specimens captured on Plum Island.

Collected species	Imma- tures	Location	Adults	Location
Diptera				
Culicidae				
—Woodland pool group				
<i>Aedes canadensis</i> (Theobald)			12	R-17
<i>Ae. stimulans</i> (Walker)			9	R-17; B-11,16
<i>Ae. aurifer</i> (Coquillett)			6	R-13,17
<i>Ae. cinereus</i> Meigen			58	R-13,17
<i>Ae. excrucians</i> (Walk.)			29	R-17,19; B-11,16
<i>Ae. fitchii</i> (Felt and Young)			40	R-6,13,16,17; B-10,11
—Floodwater group				
<i>Ae. vexans</i> (Meig.)	9	Y-6	410	R-6,7; B-3,11,15,16
—Salt marsh group				
<i>Ae. cantator</i> (Coq.)			5	R-17
<i>Ae. sollicitans</i> (Walk.)			14	R-6,12,16,17; B-3,4,15; Y-6
<i>Culex salinarius</i> Coq.	153	R-6,7; B-3	1	B-15
—Fresh water swamp group				
<i>Cx. pipiens</i> L.	106	R-6; B-3	5	R-17; B-15
<i>Cx. restuans</i> Theo.	176	B-3		
<i>Cx. territans</i> Walk.	2	R-16		
<i>Culiseta melanura</i> (Coq.)			13	R-17; B-15
<i>Cs. morsitans dyari</i> (Coq.)			837	R-6,10,17; B-1,3,11, 15,16; Y-6
<i>Cs. silvestris minnesotae</i> (Barr)			291	R-6,7,17; B-1,3,11,15
<i>Coquillettidia perturbans</i> (Walk.)			130	R-6,7,14,17; B-1,3,11,15
<i>Uranotaenia sapphirina</i> (Osten Sacken)	11	R-17	585	R-17; B-15
<i>Anopheles crucians</i> Wiedemann			1	B-11
<i>An. earlei</i> Vargas			1	R-17
—Treehole group				
<i>Ae. triseriatus</i> (Say)	48	R-6; B-3	52	R-6,7,16,17; B-3,6,11
—Rockhole group				
<i>Ae. atropalpus</i> (Coq.)	253	B-3		
Ceratopogonidae				
<i>Culicoides hollensis</i> (Melander and Brues)			2*	R-1
<i>Cul. crepuscularis</i> Malloch			1*	B-11
Tabanidae				
<i>Tabanus nigrovittatus</i> Macquart			1	R-18
<i>T. lineola</i> Fabricius			1	B-15

Table 2. Continued.

Collected species	Imma- tures	Location	Adults	Location
<i>T. sackeni</i> Fairchild			1	B-15
<i>T. fulvulus</i> Wied.			1	B-15
<i>Hybomitra lurida</i> (Fallen)			4	R-17
<i>Chrysops vittatus</i> Wied.			2	R-17; B-10
<i>C. montanus</i> Osten Sacken			8	B-6; R-17
<i>C. flavidus</i> Wied.			3	R-17; B-6,10,13
<i>C. frigidus</i> O.S.			17	R-17; B-6,15
<i>C. pikei</i> Whitney			1	B-6
<i>C. callidus</i> O.S.			1	R-17
<i>C. univittatus</i> Macq.			1	B-3
<i>C. obsoletus</i> Wied.			413	R-1,6,7,12,17,18; B-3,6,10,11
<i>C. sackeni</i> Hine			2	B-10
Muscidae				
<i>Musca domestica</i> L.			innumer- able	throughout island
<i>Stomoxys calcitrans</i> (L.)			16	R-17; B-16; Y-1,3,5,6
Sarcophagidae				
			innumer- able	throughout island
Calliphoridae				
<i>Phormia regina</i> (Meig.)	2*	R-4	innumer- able	throughout island
Cuterebridae				
	1*	Y-6	3	R-16; B-15
Mallophaga				
Philopteridae			6*	B-6,10,15
Siphonaptera				
Hystrihopsyllidae				
<i>Orchopeas howardii</i> (Baker)			21	R-6,17; B-11
<i>Ctenophthalmus pseudagyrates</i> Baker			6	R-6; B-11
Acarina				
Ixodidae				
<i>Dermacentor variabilis</i> (Say)			80	R-17,18; B-11; Y-6
<i>Ixodes dammini</i> Spielman, Clifford, Piesman and Corwin	6*	B-11		
Mammalia				
Rodentia				
<i>Peromyscus leucopus</i>			17	R-6,10,17; B-11; Y-6
<i>Microtus pennsylvanicus</i>			6	R-6; B-11; Y-6

Table 2. Continued.

Collected species	Imma- tures	Location	Adults	Location
Avian				
Passeriformes				
<i>Dumetella carolinensis</i> (L.)			14	B-6,16; Y-3,5
<i>Empidonax minimus</i> (Baird and Baird)			1	Y-5
<i>Dendroica striata</i> (Forester)			2	Y-3,5
<i>Dendroica pinus</i> (Wilson)			1	B-16
<i>Pipilo erythrophthalmus</i> (L.)			2	Y-3,5
<i>Melospiza georgiana</i> (Latham)			1	Y-5
<i>Turdus migratorius</i> L.			3	B-6,15
<i>Icterus galbula</i> (L.)			2	Y-3
<i>Sturnus vulgaris</i> L.			2	B-15
<i>Colaptes auratus</i> (L.)			7	B-10,15

* Ectoparasites: removed from host.

rant, and discarded animal cages and tires in a dump within the B-3 quadrant supported larval development of both *Aedes triseriatus* (Say), and *Ae. atropalpus* (Coquillett) (White and White 1979). This represented a new county record for *Ae. atropalpus*.

With the exception of one *Tabanus nigrovittatus* Macquart, all captured tabanids were fresh water swamp breeders. The extensive swamp land provides an ideal larval breeding habitat, especially during the mid-summer dry spell when vast areas of mud become exposed.

Eighty adult *D. variabilis* were collected during the survey, 42 males and 38 females, predominantly located at the narrowest part of the island (Y-6). The adults persisted at this area until 20 August. All *D. variabilis* were negative for rickettsiae. Six immature *Ixodes dammini* Spielman, Clifford, Piesman and Corwin were removed from both *Microtus pennsylvanicus* and *Peromyscus lecopus* hosts captured at B-11, a dense woodland. Despite extensive efforts to locate members of the argasid family, none were found.

The house fly, *Musca domestica* L. found throughout the island in the adult stage. Since it was common, collection efforts were not extensive. The stable fly, *Stomoxys calcitrans* (L.) was found in many areas of Plum Island. Most specimens were collected near the animal holding facility in the Y sector.

The flesh and blow flies were also extremely numerous. The common larval breeding source proved to be carcasses of dead birds, especially gulls.

The large gull population (2,500–3,000 birds) is reaching an “over-population” point and many of the young birds do not survive the nesting period. Various roadkills also provided excellent oviposition and breeding habitat for members of both families. No attempt was made to enumerate the prevalence of these flies.

In addition to 3 adult cuterebrid specimens captured by sweeps, a *Microtus pennsylvanicus* vole was captured that was parasitized by a larva of this family. Avian ectoparasites were not numerous. We collected 6 Philopteridae solely for inclusion into the insect collection. Only 3 specimens of *Culicoides* were captured as they attempted to feed.

All fleas were collected from their anesthetized hosts; 6 *Ctenophthalmus pseudagyrates* Baker and 21 *Orchopeas howardii* (Baker) were removed from meadow vole and white-footed mouse hosts.

All mosquito pools (10–100 mosq./pool) submitted for viral isolations were negative when screened for presence of CE, EEE, SLE, WEE and POW viruses. Blood meal analyses showed, as expected, that the avian populations were supporting the *Culiseta* species and that the rodent population was supporting the *Aedes* species.

Mammal survey.—Despite 500 trap-nights throughout Plum Island, only 2 species of mammals were captured. In addition to these widespread and fairly numerous *Peromyscus leucopus* and *M. pennsylvanicus* populations, a few wild house cats, *Felis domestica*, and bats exist on the island. Respectively, these offer a natural control against rodent and flying insect populations. Other than these four mammals, no other wild animal was found on Plum Island.

All blood smears taken from the captured mammals were negative for intracellular protozoal parasites. The serum from one *P. leucopus* reacted at 1:40 to California encephalitis virus; another *P. leucopus* serum reacted at 1:20 to St. Louis encephalitis virus. All other serological tests were negative.

Cold-blooded animals seen on the island included a few garter snakes and numerous box and spotted turtles.

Avian survey.—Birds provide the most common source of blood on Plum Island. Since such large seagull (*Larus argentatus* Pontoppidan and *Larus marinus* L.) and goose (*Branta canadensis* (L.)) populations coexist with a small mammal host pool, the majority of mosquitoes on Plum Island are preferentially bird feeders (Crans 1964; Downe 1962; Edman et al. 1972).

A total of 35 passerine birds was sampled for antibodies to domestic arboviruses (EEE, WEE and SLE), and all were negative. Almost one-half of those sampled were catbirds (*Dumetella carolinensis* (L.)), an abundant temporary Plum Island inhabitant. Other species sampled are listed in Table 2. Numerous sightings of a visiting Bald eagle (*Haliaeetus leucocephalus*

(L.) were made in mid-August. There were also 7 nesting pair of Osprey (*Pandion haliaetus* (L.)) inhabiting the island. None of the shore birds, geese or raptorial were sampled in this project.

Discussion

Of the 55 infectious animal diseases contained at the PIADC, only 13 (possibly 14) viral disease agents may be transmitted by arthropods. The known natural and experimental vectors of these diseases include the following (Berge 1975; R. Shope, YARU, New Haven, Ct., personal communication).

DISEASE	VECTOR
African Horse Sickness (AHS)	<i>Culicoides</i> , <i>Aedes</i> , <i>Anopheles</i> , <i>Culex</i> spp.
African Swine Fever (ASF)	<i>Ornithodoros</i> spp.
Akabane (AKA)	<i>Aedes</i> , <i>Culex</i> , <i>Culicoides</i> spp.
Bluetongue (BLU)	<i>Culicoides</i> spp.
Bovine Ephemeral Fever (BEF)	<i>Culicoides</i> , <i>Aedes</i> , <i>Culex</i> spp.
Eastern Equine Encephalitis (EEE)	<i>Aedes</i> , <i>Culex</i> , <i>Culiseta</i> <i>Anopheles</i> spp.
Epizootic Hemorrhagic Disease (EHD)	<i>Culicoides</i> spp., <i>Aedes aegypti</i>
Ibaraki (IBA)	Not determined
Louping Ill (LI)	<i>Ixodes</i> , <i>Rhipicephalus</i> spp.
Nairobi Sheep Disease (NSD)	<i>Rhipicephalus</i> spp.
Rift Valley Fever (RVF)	<i>Aedes</i> , <i>Culex</i> , <i>Eretmapodites</i> spp.
Venezuelan Equine Encephalitis	<i>Aedes</i> , <i>Culex</i> , <i>Anopheles</i> , <i>Mansonia</i> , <i>Psorophora</i> spp.
Vesicular Stomatitis Virus (VSV)	<i>Aedes</i> , <i>Anopheles</i> , <i>Culex</i> , <i>Lutzomyia</i> spp.
Western Equine Encephalitis (WEE)	<i>Aedes</i> , <i>Culex</i> , <i>Culiseta</i> , <i>Anopheles</i> spp.

The vectors for 2 of these diseases (ASF and NSD) have not been found on Plum Island. Furthermore, 6 diseases (BLU, EEE, EHD, VEE, VSV and WEE) can be considered domestic. Therefore, there are only 6 exotic disease agents of concern on Plum Island, i.e. AHS, AKA, BEF, IBA, LI, and RVF. Only 6 arboviral disease agents are being used in current research, i.e. AHS, ASF, BLU and RVF with AKA and IBA being studied minimally. The remaining 8 arboviruses are presently only in storage. With the excep-

tion of the vectors of ASF and NSD, all other disease vectors are represented on the island by one or more species of the above mentioned genera. That is, of course, not to assume that species of mosquitoes, ticks or biting midges from Plum Island are equally capable of transmitting the diseases as the natural vectors or those used in experimental transmission studies. There are species of *Aedes*, *Culex*, *Culiseta* and *Anopheles* present on Plum Island which are considered natural vectors of 3 diseases (i.e. EEE, VEE and WEE, all considered domestic diseases). Vectors of the remaining 9 diseases (AHS, AKA, BEF, BLU, EHD, IBA, LI, RVF, and VSV) have only nonspecific representatives of the genera implicated as natural or experimental vectors.

A potential problem exists concerning the inter-island migration of vector insect species. The absence of adequate breeding areas for *Ae. sollicitans* (Walker), *Ae. cantator* (Coquillett), *Culicoides hollensis* (Melandar and Brues) and *T. nigrovittatus* Macquart on Plum Island indicates that these species are crossing the 2 km of open sea from the closest land mass. Extensive salt marshes exist at Orient Point, the easternmost tip of Long Island's north fork and at Gardiner's Island, ca. 8 km to the south of Plum Island. Prevailing westerly winds may assist these insects in crossing Plum Gut.

Despite the simultaneous presence of disease agents and potential vectors, the prevalence of an active arbovirus in the invertebrate population becomes medically important only when there exists a coincident susceptible host population for virus amplification. With the exception of a few animals destined for research that are quarantined as they arrive on Plum Island, all research animals are housed within the high containment laboratory buildings. Other than the two rodent species, the few cats and bats, no other wild mammals exist on Plum Island. Therefore, the relative absence of suitable large animal host populations would result in nullifying a potential epizootic in a mammal population. For example, despite the abundant tabanid populations on Plum Island and the ability of certain tabanids to transmit diseases studied at the PIADC (e.g. rinderpest), if only as a mechanical vector (Bhatia 1935; Tidwell et al. 1972), the absence of a susceptible host pool renders their presence insignificant. Indeed, as Krinsky (1976) states, the role that vectors play in virus transmission maintenance is to "increase the size of epizootics in localized situations in which large numbers of acutely infected animals are in proximity to susceptible hosts." The relative absence of mammalian hosts in this particular circumstance, coinciding with an abundant avian population on Plum Island, creates a situation where the majority of the native mosquito species are feeding on birds. Thus, it appears that the relative absence of susceptible mammalian hosts and the abundance of avian hosts has resulted in influencing the abundance of potential vectors within certain genera (cf. *Aedes*, *Culiseta*). Therefore, one would expect that if Plum Island were susceptible to an arbovirus epizootic,

it would have to be through an avian route. This would be true for both native arboviruses and arboviruses used in research.

Of the arboviral agents used for research at the PIADC that can be passed through an avian route, EEE and WEE (eastern US isolates of WEE are now referred to as Highlands J virus), are generally seen annually in arbovirus surveys conducted along the east coast (Altman et al. 1967; Bast et al. 1973; Lord and Calisher 1970; Morris et al. 1973; Morris et al. 1975; Srihongse et al. 1978). Therefore, should EEE or HJ be isolated from resident or migrating birds of Plum Island, obviously it cannot be assumed that there had been a break in containment. What could be of concern is the fact that the extensive shore bird population on the island could potentially play a role in amplifying native virus (along the flyway) and supporting an avian arbovirus epizootic. In such a case, the proliferation of a native arbovirus is much more likely than a breakdown in containment of exotic disease agents.

None of the passerines sampled in this survey possessed detectable arbovirus antibodies (EEE, HJ or SLE) at a time when adjacent states reported numerous mosquito isolations (W. Crans, Rutgers University, New Brunswick, NJ and H. Maxfield, Massachusetts Department of Public Health, Middleboro, MA personal communications). Attempts to detect antibodies in both the mammal and avian specimens to diseases studied on Plum Island (except EEE and WEE) were not performed during this survey. A comprehensive attempt should be made to routinely monitor sentinel pheasants and rabbits for antibodies to arboviruses used in research at the PIADC. The proliferation of EEE or HJ viruses through the mosquito or avian cycles should not cause concern for the research facility since this can occur anywhere along the east coast of the United States where vector mosquito species and potential avian host populations overlap. What could be of concern to the facility is the possible amplification of a disease organism used in research in the prolific native avian host pool with the bird-feeding mosquitoes (*Culex*, *Culiseta* spp., etc.) acting as vectors.

In order to circumvent such an occurrence, recommendations for chemical, biological and mechanical control have been made to the PIADC staff. Incorporation of certain of these suggestions may help to alleviate potential problems. The unique proximity of foreign disease agents to native host and vector species justifiably causes concern. However, should a concerted vector control program be established on Plum Island in conjunction with regular screening of sentinel species for antibodies to diseases used in research, the chances for an epizootic become even more remote.

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New York State Department of Health, Saranac Lake District Office,
Saranac Lake, New York 12983.

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CONTROL OF *DERMACENTOR VARIABILIS*.¹ 1. LARVAL
AND ADULT SUSCEPTIBILITY TO
SELECTED INSECTICIDES

Dennis J. White and Jorge L. Benach

Abstract.—The relative susceptibility of the American dog tick, *Dermacentor variabilis*, to selected insecticides was determined in the laboratory by larval exposure to insecticide-treated surfaces and by adult exposure to topically applied insecticides. Subsequent field experiments were conducted with caged ticks to determine the potential of these insecticides for use in area control of *D. variabilis* adults. Results from both field and laboratory experiments indicate that emulsifiable formulations of naled and chlorpyrifos were highly effective acaricides, more toxic to larval and adult ticks than acephate, propoxur, pyrethrins and ronnel, as demonstrated by LC₅₀ and LC₉₀ values.

Due to the prevalence of the American dog tick, *Dermacentor variabilis* (Say), on Long Island, New York (Anastos 1947; Collins et al. 1949; Good 1973), and the recent increase of Rocky Mountain Spotted Fever (RMSF) cases on Long Island (Benach et al. 1977), we wished to determine the relative susceptibility of larval and adult *D. variabilis* to certain insecticides under laboratory conditions and to determine the efficacy of field applications of these insecticides for the control of *D. variabilis* (White et al. 1980a, b).

Local environmental legislation and court actions precluded the use of some insecticides and acaricides already labeled for area tick control. Thus, our aim in studying the susceptibility of *D. variabilis* adults and larvae was to attempt to increase the choice of insecticides available for area control. Field applications of nonlabeled chemicals for *D. variabilis* control were made possible by experimental use permits from the New York State Department of Environmental Conservation, as per Part 172 of the Federal Insecticide, Fungicide and Rodenticide Act of 1972.

This is the first of 3 reports aimed at the control of questing *D. variabilis* in areas where attachment to humans and domestic animals is most likely to occur. In this paper, we report the results of laboratory and field efficacy trials of 6 insecticides against *D. variabilis*.

¹ Acari: Ixodidae.

Materials and Methods

Larval bioassays.—Larvae utilized for bioassay experiments were reared in the laboratory from eggs obtained from field-collected engorged *D. variabilis* females. Larvae were kept in moist cotton-stoppered plastic tubes within desiccator jars containing a saturated solution of NH_4Cl . Adult ticks were collected for bioassay experiments by dragging a piece of white flannel cloth (1 m²) along vegetation adjacent to roadsides and paths in various areas of Long Island. Captured ticks were placed in moist cotton-stoppered tubes, brought to the laboratory, and maintained in the same manner as larvae.

Larval exposure to each chemical dilution was accomplished by slightly modifying techniques reported by Hansens (1956). Filter paper (12.9 cm²) was used to line the insides of 3.7 ml screw-cap vials. A uniform amount (0.15 ml) of each insecticide dilution was added directly to the filter paper in each vial. Control vials received 0.15 ml of distilled water. Ten 8- to 10-week-old unfed larvae were placed with needle-point forceps directly on the moist filter paper in each of the 12 vials. Two replicates of 5 chemical concentrations and of controls represented a test series for the laboratory bioassays.

The treated surface experiments involved emulsifiable concentrate formulations of chlorpyrifos (*O,O*-diethyl *O*-(3,5,6-trichloro-2-pyridyl) phosphorothioate) from 36 mg to 1.5 mg a.i./vial and ronnel (*O,O*-dimethyl *O*-2,4,5-trichlorophenyl phosphorothioate) from 108 mg to 10.8 μg a.i./vial, courtesy of Dow Chemical Co.; propoxur (*O*-isopropoxyphenyl methylcarbamate) from 20 mg to 20 ng a.i./vial, courtesy Chemagro naled (1,2-dibromo-2,2-dichloroethyl demethyl phosphate) from 840 mg to 840 ng a.i./vial, courtesy Chevron Chemical Co., and pyrethrins with 10% piperonyl butoxide from 1.44 mg to 144 ng a.i./vial, courtesy FMC. In addition to the above, a water soluble powder formulation of acephate (*O,S*-dimethyl acetylphosphoramidothioate), courtesy Chevron Chemical Co., was used in the topical application experiments. The same chemicals were used for field experiments.

Adult bioassays.—Topical applications of various dilutions of the insecticide emulsions proved to be the most efficient method of adult exposure to the chemical in the laboratory. Filter paper (45.1 cm²) was used to line the inside of 29.6 ml screw-cap vials. The paper in each vial was moistened with 0.5 ml distilled water to provide a source of humidity. One microliter of a chemical dilution was placed on the dorsum of each of 20 ticks (of both sexes) to be treated with that dilution. Individual ticks were restrained by forceps while the chemical was applied and held for 10 s before they were placed into the vials. Ten treated adult ticks were contained in each vial. A regimen of 2 replicates of each of the 5 chemical dilutions and controls

represented a test series for the adults. Concentrations of the applied chemicals ranged from 40,000–3,000 ppm for acephate, 3,600–1.5 ppm for chlorpyrifos, 43,500–0.4 ppm for naled, 8,200–0.82 ppm for propoxur, 50,000–500 ppm for pyrethrins with piperonyl butoxide and 7,500–75 ppm for ronnel.

Mortality, defined as the failure of a tick to respond to being breathed upon (Mount et al. 1970), was determined in all vials 24 and 48 h after initial exposure. Since ticks are negatively geotropic, all vials were maintained in a horizontal position at 24°C and a 10:14 h light:dark photoperiod throughout the 48 h test period.

Field tests.—During field experiments, postspray dragging proved to be a variable and inefficient tool (White et al. 1980b) for monitoring insecticide spray efficiency. Therefore, caged ticks were utilized to determine the efficacy of the insecticide applied under field conditions. The plots used for the field trials were open, ca. rectangular fields, ranging in size from 0.4 to 1.6 ha and dominated by 10 to 25 cm high grass vegetation. Ten adult ticks were placed inside each of 12 cylindrical aluminum wire screen cages (ca. 85 cm³, 4 cm diam × 9 cm long, mesh opening 2.25 mm²). Cages were supported by stakes 15 cm above the ground (to approximate the position of questing ticks) in rows parallel to the line of travel of the sprayer. A Buffalo Turbine mist blower, model CS, was operated at 14.1 kg/cm² (200 psi) with four 0.64-cm (¼") Tee Jet nozzles (i.e. 2, ¼ TT 6504; 1, ¼ TT 6503; and 1, ¼ TT 6502) and calibrated to deliver 28.2 l/ha (3 gal/acre). The vehicle upon which the blower was mounted had a forward speed of 8 km/h (5 mph), during spray activities. Sprays were delivered downwind when wind speed was no greater than 8 km/h. Immediately after treatment, ticks were transferred to moist cotton-stoppered plastic tubes. Mortality was then determined 24 h after chemical exposure.

Probit analyses (Finney 1964) were conducted on laboratory bioassay mortality data taken at 24 and 48 h.

Results and Discussion

The mean LC₅₀ and LC₉₀ values, as well as the standard error of the mean, determined at 24 and 48 h after exposure of the tick larvae to the corresponding insecticide, are shown in Table 1. Results of the larval bioassays indicate that, based on LC₅₀ and LC₉₀ values, naled was the most toxic of the 5 insecticides to *D. variabilis* larvae. According to the 48 h LC₉₀ values, naled is from 32× to 554× more toxic to *D. variabilis* than the remaining compounds. The 48 h LC₉₀ values of ronnel and synergized pyrethrins indicate that a substantially higher dose was necessary to result in similar mortality figures.

Data derived from the topical application experiments on adults are shown

Table 1. Mean LC₅₀ and LC₉₀ values (ppm) with standard error (SE) of the mean, determined at 24 and 48 h after exposure of *D. variabilis* larvae to surfaces treated with various concentrations of 5 insecticides.

Chemical	LC ₅₀			LC ₉₀		
	Time	Mean	SE	Time	Mean	SE
Chlorpyrifos	24	2.39	1.15	24	1.99	1.32
	48	0.21	—	48	1.29	—
Naled	24	0.02	0.01	24	0.09	0.05
	48	0.01	0.006	48	0.04	0.01
Propoxur	24	0.64	—	24	3.48	—
	48	0.58	—	48	2.87	—
Pyrethrins	24	2.64	0.16	24	44.44	3.79
	48	0.58	0.41	48	22.14	8.76
Ronnell	24	24.70	11.60	24	60.39	10.09
	48	2.97	1.25	48	13.36	2.93

in Table 2. The mean LC₅₀ and LC₉₀ values for naled and chlorpyrifos are very similar, indicating that relatively low concentrations of these materials were necessary for effective control. Synergized pyrethrins was the third most active material against topically treated adults followed by ronnel, propoxur and acephate in order of decreasing toxicity. As with the larval experiments, acephate required a very high concentration to produce mortality in *D. variabilis* adults.

Table 2. Mean LC₅₀ and LC₉₀ values (ppm) with standard error (SE) of the mean, as determined by probit analysis at 24 and 48 h after exposure of *D. variabilis* adults to various concentrations of 6 topically applied insecticides.

Chemical	LC ₅₀			LC ₉₀		
	Time	Mean	SE	Time	Mean	SE
Acephate	24	4,941.83	356.77	24	28,248.99	3,775.48
	48	2,185.00	1,441.89	48	9,745.27	448.71
Chlorpyrifos	24	7.75	0.50	24	29.84	3.65
	48	6.32	1.16	48	19.08	5.92
Naled	24	8.76	0.64	24	57.50	20.04
	48	7.26	1.04	48	27.30	6.88
Propoxur	24	182.39	15.57	24	673.72	42.52
	48	166.18	14.29	48	574.78	61.47
Pyrethrins	24	26.60	6.28	24	106.24	21.94
	48	25.32	7.56	48	97.13	12.83
Ronnell	24	185.05	35.16	24	519.87	212.73
	48	158.41	26.34	48	418.09	30.38

Table 3. Percentage mean mortality at 24 h of caged adult ticks placed at various distances from the insecticide sprayer and treated with a specific concentration of 1 of 6 insecticides.

Distance (m) from sprayer	Chemical and concentration (actual insecticide)												
	Acephate		Chlorpyrifos		Naled			Propoxur		Pyrethrins		Ronnell	
	6%	3%	0.12%	0.06%	0.36%	0.18%	0.09%	0.22%	0.11%	0.05%	0.01%	0.25%	0.12%
6	100	100	100	100	100	100	100	100	100	100	100	100	100
12	100	75	100	100	100	100	100	100	100	100	80	100	90
18	80	70	100	100	100	100	100	100	90	95	50	100	90
24	75	70	90	100	100	100	100	100	70	100	20	100	65
30	45	55	100	85	100	40	95	100	60	80	10	100	40
Control	10	5	10	5	5	10	5	0	10	0	10	5	5

As illustrated in Table 3, these same emulsifiable chemicals (acephate was formulated as WP) were used to determine relative efficacy for control of caged *D. variabilis* under field conditions. The concentrations were selected arbitrarily based on information already on the label for use under area wide outdoor application and either diluted by $\frac{1}{2}$ or doubled for additional data against the American dog tick. The higher concentrations of each insecticide produced 100% mortality in those caged ticks nearest the point of application in all cases. All concentrations of naled and chlorpyrifos were shown to be very active even when dispersed up to 24 m from the point of application. High concentrations of ronnel and propoxur were effective up to 30 m from the application point, but these concentrations may not be acceptable for area wide outdoor application. Similarly acephate required exceedingly high concentrations to produce mortality. Synergized pyrethrins at 0.05% may be effective for the control of *D. variabilis* but potential applicators should consider the cost/benefit ratios of all materials.

In addition to assessing the utility of the mist blower, the data in Table 3 indicate that both naled and chlorpyrifos are highly active for *D. variabilis*. Choice of material to be used in a control program will depend on availability of the individual materials, registration of the materials in the particular geographic area and chemical cost. These parameters aside, three compounds used in this study, chlorpyrifos, naled, and synergized pyrethrins, can be applied at acceptably low concentrations. The mortality figures produced by propoxur and ronnel show that they require slightly higher concentrations, but if the materials are available and are registered for area use, they may be effective agents for the control of *D. variabilis*. The concentrations required for acephate for effective applications were very high, and as such, does not provide a justification for using acephate against the American dog tick.

Our findings support those of Drummond et al. (1971) who also stated

that ronnel was less effective than chlorpyrifos for control of *D. albopictus* Packard. Mount et al. (1970) showed that naled was ca. 10 times as toxic as chlorpyrifos to 1- to 2-month-old *Amblyomma americanum* (L.) nymphs. However, Drummond and Medley (1965) reported that a 0.25% naled formulation was less effective than a 0.75% ronnel in controlling adult *A. americanum* on cattle. Rawlins and Mansingh (1977) indicated that naled exhibited acaricidal effects on 3 Jamaican species of livestock ticks.

The results of laboratory and field insecticide applications have shown that naled and chlorpyrifos are toxic to *D. variabilis* and, when applied under field conditions, will kill them even at concentrations of 0.09% and 0.06%, respectively.

The field caged tick study, as well as the laboratory toxicity study, strongly suggest that naled and chlorpyrifos, when applied by high-pressure, low-volume equipment, can provide control of American dog tick questing populations. Since ticks congregate along paths or roadsides (Smith et al. 1946), an effective and economical control program can be instituted with the objective of controlling populations of *D. variabilis* in these areas. If insecticide applications are made to coincide with peak tick populations (Good 1973; Smith et al. 1946) in areas of endemic RMSF activity, the objective of reducing the probability of human exposure to infected ticks can be realized (White et al. 1980a). Control efforts directed against questing ticks in infected foci could contribute to the decrease of human RMSF cases in given areas.

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New York State Department of Health, Saranac Lake, New York 12983
and New York State Department of Health, State University of New York
at Stony Brook, Stony Brook, New York 11794.

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CONTROL OF *DERMACENTOR VARIABILIS*.¹ 3. AN
ANALYTICAL STUDY OF THE EFFECT OF LOW VOLUME
SPRAY FREQUENCY ON INSECTICIDE-STRESSED
AND NONSTRESSED POPULATIONS

Dennis J. White, Jorge L. Benach, Laurel A. Smith and Soo P. Ouyang

Abstract.—Nine field plots (each 0.4–0.6 ha) were selected along the south central part of Long Island, New York, to study the effect of insecticide spray frequency on a questing *Dermacentor variabilis* population. Assignment of treatment was made according to dominant vegetation, location and tick preferential habitat. Three plots received no treatment, 3 plots were sprayed with water (3 once, 2 twice, and one 3 times) and 3 plots were similarly sprayed with an emulsifiable formulation of naled. Plots were randomly monitored for tick density at weekly intervals. A total of 2,872 ticks was collected from all plots by dragging. Multiple and simple regression and exploratory data analyses were employed to determine normal or estimated tick populations at each plot throughout the adult tick season, rate of seasonal weekly decline of tick population, and the effect of insecticide spray frequency on the questing American dog tick population. Results indicated a 20% weekly exponential decay in numbers of questing adult ticks over the 1978 season. No effect was seen due to the water treatment. One spray of naled produced an 82% reduction of the questing tick population; 2 sprays, a 95% reduction; and 3 sprays, a 96% population reduction.

Investigations on the effect of insecticides or acaricides on tick populations in the field have been reported (Hoch et al. 1971; Mount et al. 1968, 1971; Smith et al. 1946; Wharton et al. 1976). Yet, little work has been done to delineate the effect produced on seasonal populations of questing American dog ticks by a series of well timed insecticide applications. The elaborate work reported by Smith et al. (1946) is the classic description of the biology of *Dermacentor variabilis* and has provided a foundation for further research into bionomics and improved control techniques.

Extensive tick control has been most commonly practiced in areas where ticks affect livestock (Drummond 1977; Teel et al. 1977; Wharton 1976). Area control of tick species affecting humans has become of recent interest to public health agencies along the east coast of the United States due to

¹ Acari: Ixodidae.

the increase of reported Rocky Mountain spotted fever cases (Benach et al. 1977; D'Angelo et al. 1978; Hattwick 1971; Loving et al. 1978).

Preliminary laboratory and field experimentation (White and Benach 1980) indicated the susceptibility of *D. variabilis* to naled (1,2-dibromo-2,2-dichloroethyl dimethyl phosphite), a nonpersistent insecticide. The development of fast-acting non-residual insecticides has benefitted public health agencies concerned with vector control. The advantages derived from the use of nonpersistent chemicals can be enhanced by a schedule of chemical applications during a particular tick season (Clymer et al. 1970).

Because control of the American dog tick is directed to the questing population, a certain percentage of ticks may be protected from the spray technique, e.g. in the soil, on hosts, or at the bases of vegetation. The population monitoring technique most often used for *D. variabilis* (i.e., dragging) measures only the questing population. The effect of chemical sprays may not be felt by the majority of ticks in a field or plot at any particular time. Dragging has been shown to be an inefficient (White et al. 1980) tool for monitoring actual field populations, and actual estimates of field populations have to be extracted from a combination of prior seasonal population data, abiotic factors affecting a particular plot (weather, vehicle traffic, etc.), potential favorable habitat, host availability and residents' complaints. A series of chemical applications can be made to compensate for the inherent weaknesses of field tick population estimates. Ticks that happen to be at the base of some vegetation may successfully escape contact with a chemical application. However, if these and other ticks are exposed at the time of subsequent applications, chances are greater that most ticks on the plot will, at some time, be subjected to contact with the acaricide.

A series of well timed chemical applications could lead to an effective *D. variabilis* control program. The present paper discusses the effect of 3 mist applications of naled at 4-week intervals on the questing population of *D. variabilis* over a 3-month season.

Materials and Methods

During the early spring of 1978, nine field plots (0.4–0.6 ha) were selected along the south shore of central Long Island, New York. Plot selection was based on dominant vegetation, location, and likelihood of supporting large numbers of *D. variabilis*. Three plots were chosen for their grass-dominant habitat, 3 for their grass-forb mixture habitat and 3 for their grass-forb-deciduous combination habitat. All plots were grouped into triplets or blocks that were similar in composition for the 3 parameters of vegetation, location and tick preferential habitat (Smith et al. 1946; Sonenshine et al. 1972). Treatment of each of the 9 plots was allocated a random, subject to the following constraints: (1) Three plots received no treatment (C1, C2, C3);

(2) Three plots received water sprays (as a control for the application procedure), 3 plots sprayed once (W1), 2 plots sprayed twice (W2) and 1 plot sprayed 3 times (W3) during the season; (3) Three plots received naled sprays, 3 plots sprayed once (D1), 2 plots sprayed twice (D2) and 1 plot sprayed 3 times (D3) through the adult tick season. Assignment of spray frequency among the 3 water-sprayed plots and 3 naled-sprayed plots was made at random. (See Table 1.)

A 24 (c) registration was received by Chevron Chemical Co. for the use of Dibrom 8 (naled) to control the American dog tick (EPA SLN No. 780008). Treatment for the D1, D2 and D3 plots consisted of application of 168 g actual Dibrom per ha (0.15 lbs/A). The naled formulation (1,2-dibromo-2,2-dichloroethyl dimethyl phosphate) was supplied courtesy of Chevron Chemical Co. Both water and chemical applications were delivered as previously described (White and Benach 1980). Plots to be sprayed once were sprayed during wk 1; plots sprayed twice were treated during wk 1 and 5; the plot sprayed 3 times was treated during wk 1, 5 and 9.

Weekly tick collections were made at each plot. Ticks collected at plot C3 were returned to the laboratory. On those plots that were treated during a specific week, collections for that week were made 24 h after the spray. White flannel cloth (1 m²) was used to collect questing ticks by dragging. Ticks attached to the flannel drag were counted every 10 m along a predetermined line of travel at the roadside edge of each plot (60–100 m).

All 9 plots could not be monitored for tick population on 1 day. Therefore, the group of plots was divided into 3 sets of 3 plots, each of which would be randomly monitored on 3 successive days of the week. In order to control for the effect of measuring the plots at different times of day and on different days of the week, predetermined random schedules were made resulting in 72 combinations of tick collection sequences in control, water-sprayed and naled-sprayed plots.

Statistical analyses were conducted using a randomized block analysis of variance model where blocks were similar for plot location, dominant vegetation and tick density. For analysis purposes, actual tick counts in each plot were normalized and transformed to base 10 logarithms. Analysis of data was conducted by 3 separate techniques; exploratory data analysis (Tukey 1977), multiple, and simple regression utilizing the analysis of variance model.

Actual field questing tick population data (Table 2) obtained by dragging were subjected to the following transformation:

$$Y_{ijk} = (X_{ijk}/N_{ij}) \times 100$$

Where i = indicator for treatments, i.e., $i = 1$ for control groups, $i = 2$ for water-treatment groups, and $i = 3$ for naled-treatment groups; j = the indicator for blocks, i.e., $j = 1$ for block 1, $j = 2$ for block 2, etc; and k is the

Table 1. Vegetational composition and number of *Dermacentor variabilis* collected at each of the 9 study plots over the entire season.

Plot	Vegetation*	No. ticks collected	Total no./treatment
C-1	g-f	261	
C-2	g	316	
C-3	g-f-d	526	1,103
W-1	g	11	
W-2	g-f	1,034	
W-3	g-f-d	80	1,125
D-1	g-f	65	
D-2	g	185	
D-3	g-f-d	394	644
		total	2,872

* g = grass, f = forb, d = deciduous.

index for week sequence. Therefore, X_{ijk} is the original total count of ticks in treatment i , block j and week k ; N_{ij} is the number of intervals in block j , treatment i from which ticks were collected and Y_{ijk} is the transformed total count of ticks in treatment i , block j and week k .

Then, in order to stabilize the week-to-week variability within plots, the transformed data were normalized using a log transformation:

$$Z_{ijk} = \log_{10}(Y_{ijk} + 1).$$

In view of the fact that each plot had varied original (pre-experimental) questing tick populations due to the dominant vegetation, and the plots were monitored for tick counts on a random basis over a 3-day period, a median polish process was utilized to produce a range of values about a 0.0 residual value (expected questing tick counts at a given point in time, Tukey 1977).

Because both C1 and W1 plots supported very few ticks, the data gathered during the same season from plot MR (White et al. 1980) replaced the data from C1. Data from plot W1 were dropped completely so that all analyses of effect of water were conducted on data from 2 plots, W2 and W3.

Results and Discussion

Dominant vegetational characteristics of each of the 9 plots and numbers of ticks collected in each plot throughout the 12-week experiment are listed in Table 1. All captured ticks (other than C3) were released in the 10 m section of each plot from which they were collected.

Exploratory data analysis.—By analyzing the transformed data for effect of week on the questing tick population (i.e., numbers of ticks over time),

Table 2. Actual numbers of questing *Dermacentor variabilis* collected from each plot during the 12-week study.

Week	Plot									
	MR*	C1	C2	C3	W1	W2	W3	D1	D2	D3
1	49	4	102	56	2	69	15	3	12	35
2	33	4	46	60	6	107	21	7	38	128
3	28	0	45	145	1	98	14	7	27	120
4	20	0	1	50	1	101	6	6	41	62
5	23	4	47	114	1	109	4	6	1	2
6	25	2	23	36	0	141	4	10	3	12
7	10	0	13	21	0	145	3	2	13	11
8	16	0	17	12	0	76	3	7	21	18
9	25	0	7	20	0	84	3	5	15	1
10	15	0	4	5	0	53	4	2	5	1
11	4	0	4	4	0	33	3	5	3	1
12	13	0	7	3	0	18	0	5	6	3

* MR = mark-recapture (White et al. 1980).

the fitted equation produced by exploratory data analysis is $Y = 0.5549 - 0.0913X$ which indicates an exponential decay rate of 19% ($10^{-0.0913} - 1 = 0.8104$, $1 - 0.8104 = 0.1896 = 19\%$) on the original scale (actual field collection data) which explains 88% of the variability of week effects ($F = 74.312$, d.f. = 11, $\alpha = 0.01$, $R^2 = 0.88$). By holding week and plot effect fixed, a noticeable drop of tick populations is apparent in plots D2 and D3 after treatment while control plots and water-treatment plots show no such relationship. The residual value indicates the transformed tick count that, based on data gathered from the control plots, would be expected to be present during each week. Values in excess of this threshold value indicate a population of ticks larger than that which would be expected; negative values indicate populations less than that which would be expected. Also evident is a resurgence of tick populations in the D block of plots shortly after the spray until the next chemical treatment.

Multiple regression.—By employing a more definitive analysis in a multiple regression process ($F = 3.369$, 75 df, $P = 0.00$, $R^2 = 0.4733$), further significant relationships can be shown to exist. Although the model is extremely complex and encompasses effects of individual treatments in each plot, the overall week effect and treatment effect are not easily distinguishable. The same transformed and normalized data were also used for this approach. The effect of week on tick populations is similar to that which resulted from exploratory data analysis with a 21% exponential decay rate of actual tick numbers ($F = 96.48$, 11 df, $\alpha = 0.01$, $P < 0.001$, $R^2 = 0.906$). However, a rebound (due to recruitment) of the tick population occurs dur-

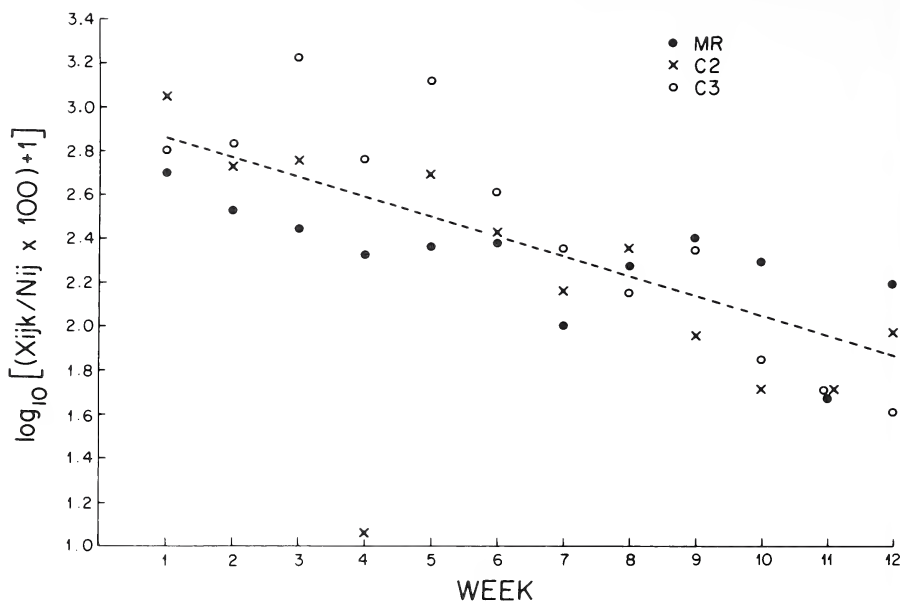


Fig. 1. Simple regression estimation of week effect on questing *Dermacentor variabilis* population transformed data.

ing weeks 5 and 8. The effect seen on the field tick populations by the water treatments was variable and probably due to the week effect included in this analysis. However, an 82% decrease of the questing tick population was seen after 1 application of naled on all 3 plots. On the two plots, D2 and D3, that were sprayed twice (during weeks 1 and 5), a reduction of 96% occurred. Likewise, an 87% reduction occurred on the plot that was sprayed for the 3rd time during week 9.

Simple regression.—By using a simple regression analysis the results become more clarified because each effect (week or treatment) is removed individually. For example, through use of the control groups to estimate the week effect on tick populations, the week effect can be extracted from the water-treatment group and the naled-treatment group to determine more precisely the effect of such treatment. Therefore, because the week effect has now been determined without the introduction of insecticide or mechanical stress on the population used for analysis, the actual results are more practical. Now the equation fitted for week effect becomes:

$$Z_{ijk} = 2.9252 - 0.0976X \quad (\text{See Fig. 1})$$

$$F = 33.2983. \quad 35 \text{ df}, \alpha = 0.05, P < 0.01$$

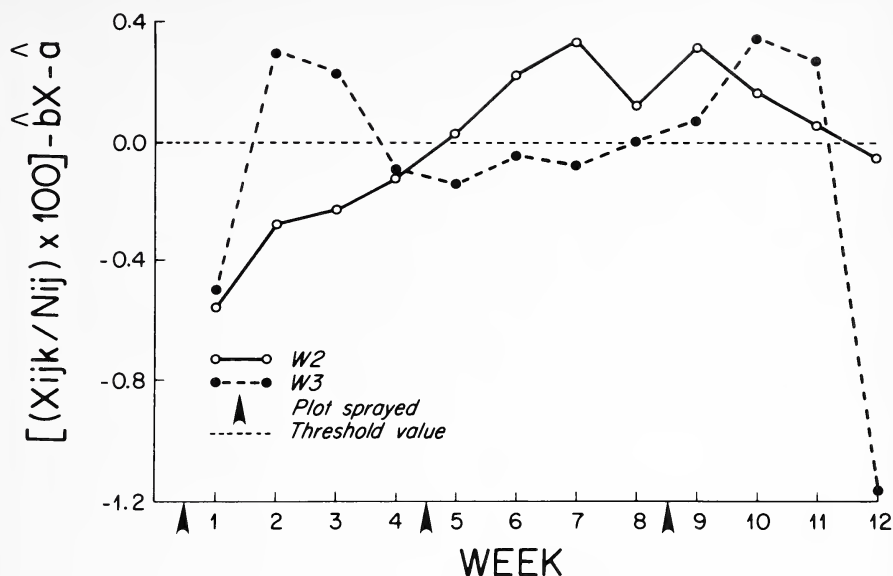


Fig. 2. Effect of water treatment on questing *D. variabilis* populations.

or, that the week effect on the tick population is exponential decay with a rate of 20% ($10^{-0.0976} - 1 = 0.7987$. $1 - 0.7987 = 0.2013 = 20\%$).

By extracting the week effect from the data gathered from the water treatment analysis, the effect of water on the tick population is nonexistent (Fig. 2). By extracting the seasonal tick reduction figures (week effects) from the data gathered from the naled treatment analysis, the effect on the questing tick population is pronounced (Fig. 3). Obviously, the effect of the 1st naled spray cannot be determined by simple regression because extensive tick sampling was not conducted prior to week 1. The 2nd naled spray reduced the population by 95% while the 3rd spray resulted in a 96% tick population reduction.

The preliminary laboratory and field experiments performed by White and Benach (1980) led to the conclusion that naled could prove effective in a large scale control program directed against *D. variabilis*. However, because naled is nonpersistent, a control program would have to rely on a series of well timed chemical applications over an entire season. For example, although all ticks were removed from plot C3 each week (Table 2), a large number of ticks were captured the following week, indicating 1 or both of the following: a large immigration factor or a poor sampling technique (White et al. 1980). In order to reduce tick numbers over an entire season, control should be carried out in a series of applications timed so

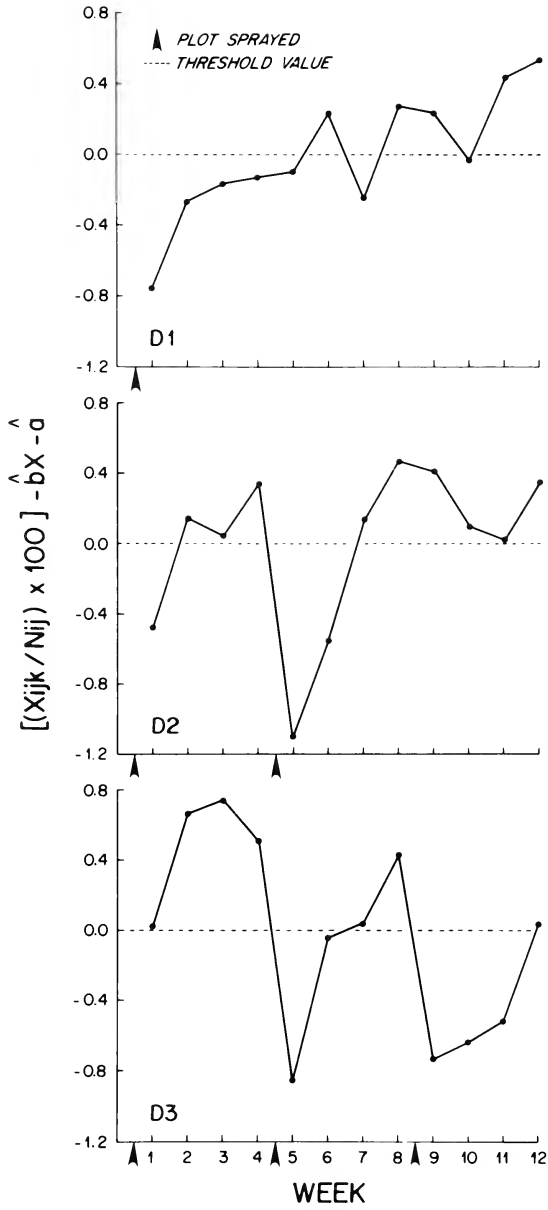


Fig. 3. Effect of naled treatment on questing *D. variabilis* populations.

that ticks do not reach a threshold value and so that chemicals are applied cost-effectively.

As can be seen in Table 1, tick densities were greatest in either the grass-forb or the grass-forb-deciduous mixed habitat than in grass alone. The greatest proportion of ticks present in the plots was seen in the first 4–7 weeks of the study, again dependent on the habitat. By incorporating all population data from the control plots (MR, C2 and C3, Table 2) a regression analysis resulted in the week effect, or effect of time within a season on the natural or nonstressed tick population. Over the season of study, a weekly exponential decay rate of 20% explained the general tick population depletion through mid-August and therefore represented our weekly threshold value.

By removing this week effect from the treatment effect (simple regression), a more precise description can be made. After each application of naled, there was an immediate decrease in the tick population followed by a gradual resurgence over the next 3 weeks. This would be expected because naled is efficient but nonpersistent. As the tick population increases to the expected value (0.0, Fig. 3), the effect of the previous naled spray has been eliminated at that point. An increase beyond the expected value necessitates a reapplication of naled to further reduce the questing population. The 2nd naled application resulted in a 95% and 97% reduction on plots D2 and D3 while the tick population continued to increase in D1.

After the 2nd spray, tick populations again started to increase to the expected value at a more rapid recovery. Within 2 weeks, the tick population recovered to the point where they exceeded the expected values in both plots D2 and D3. During week 6 and week 9 plot D1 was mowed, which brought the tick population below what was expected, an unintentional control mechanism. Plot D3 received the 3rd application of naled during week 9, which resulted in a 96% reduction of questing ticks. The recovery was now much slower, from week 9 through 12. The effect of the physical act of treating the ticks along roadside edges with water (W2, W3, Fig. 2) is negligible.

Although each individual analysis provided both significant statements and generalizations concerning the experiments, one analysis followed the other in a logical sequence to determine the most significant statements. Exploratory data analysis provided the justification for the transformation (Tukey 1977) of the raw data to stabilize the variances (plot to plot, week to week, etc.), and for the median polish to account for differences of pre-experimental tick populations. This analysis provided an insight into results that were confirmed by classical regression techniques. The multiple regression and simple regression resulted in almost identical statements (e.g. 20%

population decay rate). Simple regression assumed variable independence while the multiple regression did not.

Conclusions derived from all analyses are in agreement. There is an overall decline of the tick population during a season of about 20% per week, within the range reported by White et al. (1980). Spraying water on ticks had no effect on the population so treated. Low-volume sprays of naled resulted in dramatic drops of the population (82–97%) followed by gradual recovery, consistent with the mark-recapture study (White et al. 1980) recruitment phenomenon. Cutting of grass along tick habitats was statistically shown to reduce the expected questing tick population for a short term.

Acknowledgments

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(DJW) New York State Department of Health, Saranac Lake, New York 12983; (JLB) New York State Department of Health, State University of New York at Stony Brook, Stony Brook, New York 11794; and (LAS and SPO) Department of Applied Mathematics, State University of New York at Stony Brook, Stony Brook, New York 11794.

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FURTHER EVIDENCE FOR CHLORPYRIFOS TOLERANCE AND
PARTIAL RESISTANCE BY THE JAPANESE BEETLE
(COLEOPTERA: SCARABAEIDAE)

Sami Ahmad and Yuen-Shaung Ng

Abstract.—Dosage-mortality responses of third-instar grubs of the Japanese beetle, *Popillia japonica* Newman, showed that a population from Fairfield (Conn.), when compared at the LD_{95} , is ca. $42\times$ as tolerant to chlorpyrifos as those from Adelphia (central N.J.; a standard susceptible population). Moreover, the 95% conf. intervals of the LD_{50} and LD_{95} of the Fairfield population did not overlap with those of the Adelphia population. Another population from Rivervale (northern N.J.) also showed 6.8-fold greater tolerance to chlorpyrifos, however, the conf. intervals of its LDs did overlap with those of the susceptible strain. The Fairfield population was characterized as "partially-resistant," and that from Rivervale as "tolerant," to chlorpyrifos.

The grubs of the Japanese beetle, *Popillia japonica* Newman, are highly destructive to turfgrass in several states east of Mississippi River (Fleming 1972). Chlordane was first used for grub control in 1947 (Fleming 1950), and since then for nearly twenty-five years chlordane and other cyclodiene insecticides, e.g., dieldrin and heptachlor, afforded good protection against Japanese beetles. Beetle resistance to cyclodienes was first reported in 1973 from Ohio (Niemczyk and Lawrence 1973), New York (Tashiro and Neuhauser 1973), and Pennsylvania (Anon. 1973). Subsequently, cyclodiene resistance among beetle populations of Connecticut (Dunbar and Beard 1975), and New Jersey (Ahmad and Das 1978) also were documented. Furthermore, because of environmental concerns the use of highly persistent cyclodiene insecticides has been restricted by the Environmental Protection Agency. Consequently, nonpersistent organophosphorus insecticides, chlorpyrifos, diazinon and trichlorfon have replaced cyclodienes for control of the Japanese beetle.

In 1977, a population of the Japanese beetle from New Jersey (Rivervale) was suspected of increased tolerance to chlorpyrifos (Ahmad and Das 1978). The following year, the greater tolerance of chlorpyrifos by the Rivervale beetle was confirmed by more extensive tests, using susceptible beetles for comparison (Ng and Ahmad 1979). We now provide additional evidence for a much greater chlorpyrifos tolerance in a Connecticut population of the beetle, compared to the New Jersey insects.

Materials and Methods

Third-instar grubs of the Japanese beetle from Fairfield, Conn. (Brooklawn Country Club golf course) were supplied by A. M. Radko (U.S. Golf Assocn., Far Hills, N.J.) on October 1, 1979. The grubs were held in the laboratory for ca. 48 hr period and then tested for susceptibility to chlorpyrifos. The procedure and laboratory conditions for the maintenance of the grubs were exactly the same as reported earlier (Ahmad and Das 1978). For comparisons of susceptibility levels, grubs were collected from a chlorpyrifos-tolerant population in Rivervale (northern N.J.; Country Club golf course), and a standard susceptible population from Adelphia (central N.J.; Soils and Crops Res. Ctr., Rutgers Agric. Exp. Stn.) on October 7 and 13, respectively. Grubs from these two populations also were held in the laboratory for ca. 48 hr prior to screening for chlorpyrifos susceptibility.

The grubs were treated topically with one-microliter drops of chlorpyrifos solutions, in 5 replicates, 10 grubs per replicate. Each test was repeated twice and the data were pooled for analyses. Solvent controls were included. The composition of the insecticide solvent, and the technique for the bioassay including that for grub rearing, were as reported earlier in detail (Ahmad and Das 1978). Mortality was recorded on 8th post-treatment day since the duration of the acute toxicity of chlorpyrifos in the Japanese beetle is 7 days (loc. cit.). Mortality data were corrected for deaths in the control group by Abbott's formula, and subjected to probit analysis according to Finney (1964). The regression coefficients (slopes) for the log dose-probit (*ldp*) lines of the 3 populations also were analyzed for statistical difference.

Results and Discussion

The dosage-mortality responses of the Japanese beetle grubs from Adelphia (N.J.), Rivervale (N.J.) and Fairfield (Conn.) are shown in Fig. 1. The LD values and their 95% confidence intervals are presented in Table 1. The Rivervale population shows a 6.8-fold greater tolerance to chlorpyrifos at the LD₉₅ level to that of the susceptible population. Tests with adult beetles also have shown the Rivervale population to be more tolerant to chlorpyrifos than the Adelphia insects (Ng and Ahmad 1979). A 4.3× greater tolerance was discerned with a significant difference between the regression coefficients (*b*) of the *ldp* lines of the two populations (loc. cit.). In the present investigation involving third-instar grubs, the regression coefficients of the *ldp* lines of the Rivervale (*b* = 0.96) and Adelphia (*b* = 2.43) populations also were found to be significantly different [*t* (*df*, 5) = 11.315, *P* < 0.05]. Thus our earlier conclusion that there were more chlorpyrifos-tolerant individuals in the Rivervale population than in the Adelphia population (Ng and Ahmad 1979) was reaffirmed. The data on chlorpyrifos tolerance of the

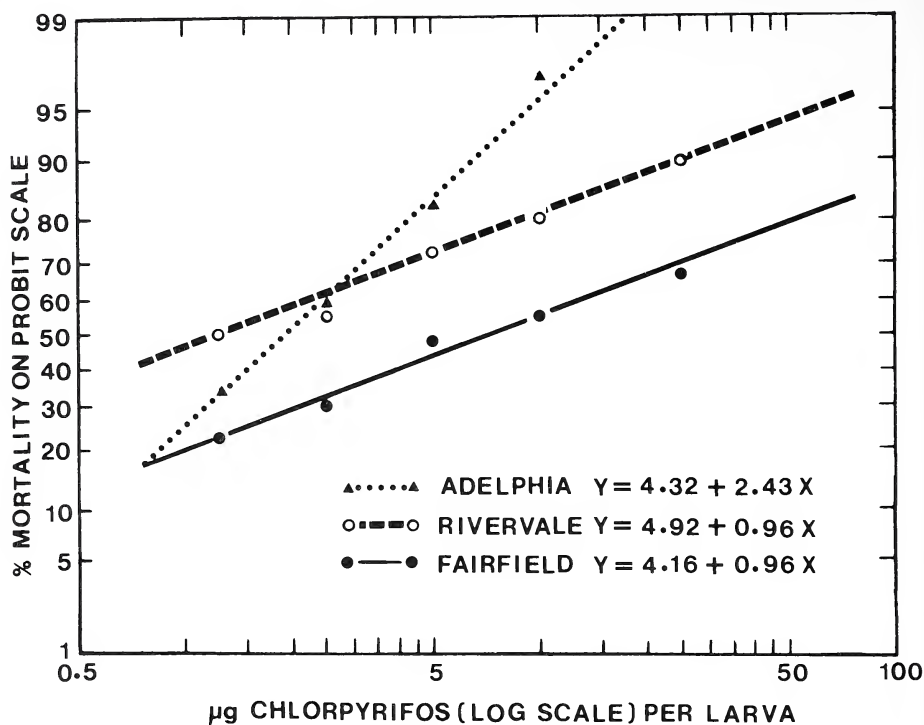


Fig. 1. Dosage-mortality responses of third-instar grubs of the Japanese beetles from Fairfield (Conn.), Rivervale (northern N.J.), and Adelphia (central N.J.); 1979.

Rivervale beetles are typical of a "tolerant" insect population showing incipient resistance to an insecticide (Busvine 1971).

Table 1 also indicates that by comparison to the Rivervale population, grubs from Fairfield are exceedingly tolerant to chlorpyrifos. At the LD_{95} level the Fairfield insects are ca. $42\times$ as tolerant as the susceptible Adelphia population, and ca. $6\times$ more tolerant than the Rivervale population. As can be expected the regression coefficient of the ldp line of the Fairfield ($b = 0.96$) grubs was significantly different to that of the Adelphia ($b = 2.43$) population [t (df , 5) = 10.145; $P < 0.05$]. Moreover the 95% C.I.s of the LD_{50} and LD_{95} of the Fairfield population showed no overlap to the corresponding C.I.s of the Adelphia insects. Taken together, these data clearly show that the selection towards more chlorpyrifos-tolerant individuals in the Fairfield population has progressed further than in the chlorpyrifos-tolerant Rivervale population.

According to Dyte and Blackman (1967) if a population of insects is re-

Table 1. Comparison of chlorpyrifos susceptibility of third-instar grubs of the Japanese beetle from Fairfield (Conn.), Rivervale (northern N.J.), and Adelphia (central N.J.); 1979.

Population ^a	LD ₅₀ ^b	LD ₉₅ ^b	LD ₉₅ ratio
Adelphia	1.90 (1.45–2.56)	9.17 (5.50–15.42)	1
Rivervale	1.20 (0.50–2.84)	62.45 (13.29–293.50)	6.8
Fairfield	7.50 (4.42–12.58)	388.06 (45.29–3,324.30)	42.2

^a Mean weight of the grubs (N = 10) were 208 mg (±25 SD) for Adelphia, 196 mg (±39 SD) for Rivervale, and 185 mg (±24 SD) for Fairfield populations.

^b Confidence intervals (*P* = 0.05) in parentheses.

sistant to an insecticide, the LD_{99,99} of the resistant strain must be significantly greater than that of the susceptible strain. From the dosage-mortality data in Table 1, we computed the lower C.I. for the LD_{99,99} of the Fairfield grubs to be 579 µg/grub; this did not overlap with the upper C.I. of the LD_{99,99} of the Adelphia population, 221 µg/grub. Thus the Fairfield population appeared to meet the requirement for characterization as a resistant population. On the other hand, as mentioned above the regression coefficient of the *ldp* line for the Fairfield population was considerably flatter than that of the Adelphia population. A flat *ldp* line is often indicative of the genetic variability in insecticide susceptibility of a population. A truly resistant population typically depicts steep slope as is usually the case with a homogeneous susceptible population (Busvine 1971). Therefore, it would be premature to assume that the entire population from Fairfield is resistant to chlorpyrifos, but rather it is an example of a partially-resistant field population, with more resistant insects in the population than susceptible ones. The Fairfield population obviously has the potential for rapidly becoming a highly resistant field population under further selection against chlorpyrifos.

Selection of a population against an organophosphorus insecticide often confers resistance to other organophosphorus compounds (Perry and Agosin 1974). There is some indication that Japanese beetles may develop resistance to organophosphorus compounds other than chlorpyrifos. For example, trichlorfon and diazinon were as ineffective as chlorpyrifos during 1979 against the grubs of the Fairfield population (A. M. Radko, pers. commun., 1979). On the other hand, trichlorfon afforded good protection against the Rivervale grubs that are substantially more susceptible to chlorpyrifos than the Fairfield population (W. Gaydosh, pers. commun., 1979).

In a previous report (Ng and Ahmad 1979), we had also shown the greater inherent tolerance ($2.1\times$) by the Rivervale beetles to bendiocarb, a potential carbamate insecticide for grub control. Although we did not test bendiocarb against the Fairfield strain, the possibility exists, that with time, the Japanese beetle populations also may become resistant to carbamate insecticides. This would not be surprising since the mode of action and detoxication mechanisms associated with tolerance and resistance are common to both organophosphorus and carbamate insecticides (Perry and Agosin 1974; Plapp 1976).

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Department of Entomology and Economic Zoology, New Jersey Agricultural Experiment Station, Cook College, Rutgers—The State University of New Jersey, New Brunswick, New Jersey 08903.

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OCHLERINI, A NEW TRIBE IN DISCOCEPHALINAE
(HEMIPTERA: PENTATOMIDAE)

L. H. Rolston

Abstract.—Ocherini is proposed as a new tribe of Discocephalinae. The tribe is characterized and 23 genera assigned to it.

The discocephalines, which are restricted to the Western Hemisphere, have been variously treated as a subfamily of Pentatomidae or a tribe of Pentatominae. Rolston and McDonald (1979) regarded this group as a subfamily and provided a diagnosis based primarily on the apparent origin of the labium, usually caudad of the anterior limit of the eyes, and the position of the trichobothria on sternite vii, the mesial member of each pair being on or, most often, laterad of an imaginary line projected tangentially along the lateral margins of the spiracular openings on sternites vi and vii. These authors removed all Western Hemisphere genera except *Brochymena* from Halyini in Pentatominae, placing *Caracia* Stål, *Marghita* Ruckes and *Janeirona* Distant in Pentatomini and the remaining genera in Discocephalinae. Those genera placed in Discocephalinae form a new tribe, for which a name and diagnosis are here provided, that is characterized primarily by the shallowly excavated or flattened superior surface of the third tarsal segment of the hind legs in females and sometimes in males as well. Members of this tribe are with few exceptions recognizable by their dull black or fuscous coloration, while the remaining genera of discocephalines, which constitute the nominate tribe, are brown, often mottled with black, or shiny black.

Ochlerini Rolston, new tribe

Type genus.—*Ochlerus* Spinola, 1837.

Diagnosis.—Superior surface of third tarsal segment of hind legs shallowly excavated in females and sometimes in males (only flattened in *Adoxoplatys*).

Trichobothria on at least last sternite laterad of adjacent spiracles, rarely with mesial trichobothrium of each pair on last sternite on line tangential to spiracle openings on last two sternites. Labium usually arising on or posterior to plane transecting head at right angle to longitudinal body axis and at anterior limit of eyes.

Basal segment of rostrum projecting caudad of bucculae, terminating on prosternum. Mesosternum thinly carinate mesially, metasternum usually so

but sometimes weakly tectiform, flat or sulcate. Metapleural ostioles each accompanied by auricle, this often somewhat elongated but not drawn out into ruga. Scutellum longer than wide at base (brachypterous forms excepted). All tibiae broadly sulcate. Spiracles present on paratergite 8 of females, on sternite 8 of males.

Comments: Among Western Hemisphere pentatomids the tarsal character state appears unique to this tribe. The location of the trichobothria laterad of the adjacent spiracle on the last sternite is characteristic of Discocephalinae, but this character state is also found in a few members of Pentatominae. The labial origin posterior to the anterior limit of the eyes is apparently constant in Discocephalini but variable in Ochlerini. All of the character states enumerated in the last paragraph of the diagnosis are constant in Ochlerini, as far as known, but various combinations of them appear elsewhere.

The following genera are placed in Ochlerini:

<i>Adoxoplatys</i> Breddin	<i>Miopygium</i> Breddin
<i>Alathesus</i> Dallas	<i>Moncus</i> Stål
<i>Alitocoris</i> Sailer	<i>Neadoxoplatys</i> Kormilev
<i>Audintella</i> Spinola	<i>Ochlerus</i> Spinola
<i>Brachelytron</i> Ruckes	<i>Orbatina</i> Ruckes
<i>Eritrachys</i> Ruckes	<i>Paralincus</i> Distant
<i>Herrichella</i> Distant	<i>Parochlerus</i> Breddin
<i>Lincus</i> Stål	<i>Pherecles</i> Stål
<i>Macropygium</i> Spinola	<i>Schaefferella</i> Spinola
<i>Melambyrsus</i> Breddin	<i>Schaderia</i> Ruckes
<i>Melanodermus</i> Stål	<i>Tetrochlerus</i> Breddin
<i>Minilincus</i> Ruckes	

I have examined species, usually the type species, of all of the above genera except *Audintella* and *Melambyrsus*. These two monotypic genera are included in Ochlerini on the basis of their descriptions.

The 23 genera of Ochlerini contain only 70 described species, but examination of a few collections reveals several undescribed genera and species.

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Dr. F. J. D. McDonald's skill in dissection and knowledge of pentatomoid genitalia contributed much to this work.

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Department of Entomology, Louisiana Agricultural Experiment Station,
Louisiana State University, Baton Rouge, LA 70803.

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NOTES ON THE BIOLOGY OF A COMMON SUNFLOWER BEE,
MELISSODES (EUMELISSODES) AGILIS CRESSON

F. D. Parker, V. J. Tepedino and G. E. Bohart

Abstract.—*Melissodes agilis*, an anthophorid bee that is oligolectic on sunflowers, was found nesting in and adjacent to a planting of commercial sunflowers in northern Utah. Observations and excavation of nests yielded information on nest architecture, larval morphology, foraging activity, and parasites. The species will probably be most valuable as a commercial pollinator where minimum- or no-tillage agricultural practices are appropriate.

Introduction

The commonest native bee species frequenting sunflower (*Helianthus* spp.) in the western United States is *Melissodes agilis* Cresson, a ground-nesting member of the Anthophoridae. Although *M. agilis* is probably responsible for a significant proportion of sunflower pollination throughout the west (Parker 1981a, b), biological information on this commercially important species is limited to a brief note on the nest tumulus and length of the main burrow (Rau 1922) and a comment by Custer (1928) that a female *Melissodes* (presumed to be *M. agilis*) entered a nest of *Svastra obliqua* (Say), another anthophorid bee. During the summer of 1979, large numbers of *M. agilis* were observed visiting and nesting in our plantings of commercial sunflowers in northern Utah; and we took the opportunity to study the biology of this species. Specifically, we provide information on nest architecture, larval morphology, nest associates, seasonal occurrence, foraging activities, and sleeping aggregations of males.

Nesting Site

Melissodes agilis nested in and between irrigation furrows in a 1-acre (0.4047-ha) plot planted to sunflowers (*Helianthus annuus* variety *macrocarpus* (D.C.)) and summer squash (*Cucurbita pepo* L.) near Logan, Utah, during July and August 1979. The site was nearly flat and the soil type was Millville Silt loam. More than 20 nests of *M. agilis* were marked with stakes and some were excavated in September. The nests appeared randomly distributed throughout the sunflower and zucchini plots; a few were as close together as 12 cm. The following description of the nests was taken from 6 excavated nests with cells.



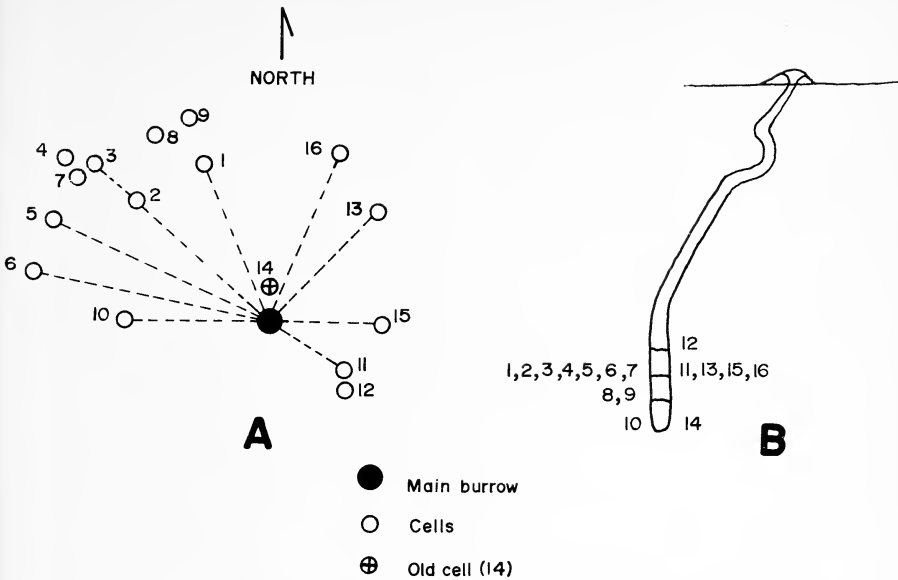


Fig. 3. Diagram of typical *Melissodes* nest. A. Arrangement of cells. B. Cross section of nest with depth of cells indicated.

Nest Architecture

No bees were observed initiating nest excavation; nests were located by observing bees entering or leaving their nests or by observing the newly excavated crater-like tumuli. The mound of soil from a typical nest excavation measured 5 cm across and 1.5 cm high. However, tumuli were not always evident. The entrance hole was in the middle of the crater and averaged 7 mm in diameter (Fig. 1). The entrance hole was not plugged during nest provisioning.

When we excavated the nests, the main and lateral burrows were filled with soil, but the main burrow could be traced by blowing out the soil and refilling it with plaster of Paris powder. Typically, the main burrow was 7 mm in diameter and spiraled downward for 4 cm before descending nearly vertically to a depth of about 12 cm (range 11–17 cm), where the first cell was placed. The main burrow was unlined, but the walls were smooth. It

←
Figs. 1, 2, 4–6. 1. Nest entrance and tumulus of *Melissodes*. 2. Compacted soil in filled *Melissodes* burrow. 4. Waxed lined cell of *Melissodes*. 5. Tops of 2 *Melissodes* cells exposed during nest excavation. 6. Overwintering *Melissodes* larva in cell; cocoon cut away to expose layers of the cocoon.

was not possible to trace the route of the lateral branches because they were filled with tightly packed soil (Fig. 2). Lateral burrows were from 1 to 10 cm in length and radiated away from the main burrow (Fig. 3). In one nest, the cells were distributed in a pattern indicating that at least 12 lateral burrows diverged from the central main burrow. Since the cells were found at 8 levels (Fig. 3), it appeared that most of the laterals were begun at different levels.

The number of cells/nest ranged from 1 to 27 ($\bar{x} = 11.5$). Cells were found at depths ranging from 11 to 19 cm below the soil surface. In multi-celled nests, some cells were about 1 cm below an adjacent one, an indication that some lateral burrows contained more than one cell.

Cell Structure and Morphology

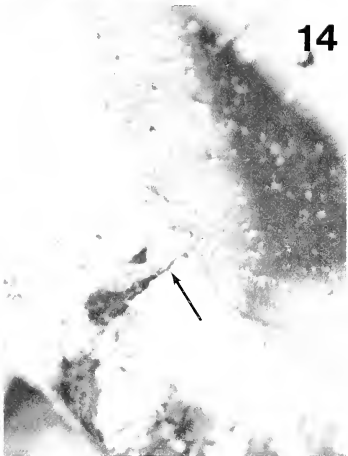
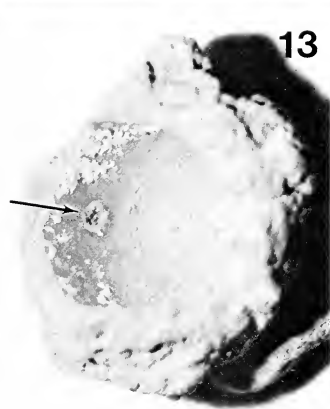
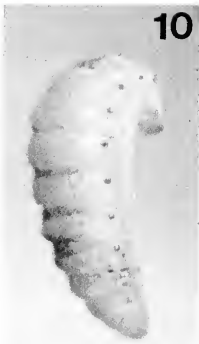
The oval cells were vertical in orientation. Each cell was 7–8 mm wide at its greatest diameter and 8–14 mm long (Fig. 4). Cell walls were made by the bee compacting about 2 mm of soil against the “roughed-out” original excavations. Following this, the inner walls (Except the cell cap) were coated with wax. The wax lining was evenly applied to all cell walls and was thick enough to be readily scraped off with an insect pin. The upper $\frac{1}{3}$ of each cell was paler and slightly rougher than the basal portion. The area of overlap between these color bands was darkened. The cell cap was composed of rings of soil, but the precise pattern could not be determined since the top of every cell was at least partially destroyed during excavation. In all cells examined, the pollen provisions had been consumed.

Most fecal material was incorporated into the cocoon layers, but at the top of the cell were some loose, concentric, tubular strands of fecal pellets in a 3 mm thick layer (Fig. 5). The larva started the cocoon by first lining the cell walls (except the top) with a thin varnish of silk. Over this layer it smeared successive, longitudinally directed strands of yellowish fecal material, separated but held together by layers of silk. Inside the fecal layer the larva produced a shiny inner cocoon of thin, transparent, yellowish silk (Fig. 6), in which it embedded a network of larger, darker strands. This inner envelope was entire and of uniform thickness and its inner surface was smooth and shiny. It was surmounted by a dome-shaped cap composed of several sheets of silk loosely held together.

The overwintering prepupal larvae were creamy white and rather flaccid.

→

Figs. 7–14. 7–8. Overwintering *Melissodes* larvae. 7. Lateral view. 8. Larvae tilted to illustrate lateral lobes. 9–10. *Triepeolus* prepupae. 9. Ventral view. Note head capsule of 1st instar larva (arrow). 10. Lateral view. 11–12. Cells with *Triepeolus*. 11. Basal ring (arrow) that holds prepupa. 12. Prepupa surrounded by fecal pellets. 13. Puncture in cell wall made by *Triepeolus*. 14. Egg chamber of *Triepeolus*. Note shriveled egg chorion.



They were C-shaped and vertical with their weight resting on the postero-dorsal area (Figs. 7, 8).

Nest Associates

Three nests contained a total of 7 cells parasitized by the cuckoo bee *Triepeolus helianthi* (Robertson). The distinctive rigid prepupae (Figs. 9, 10) were held erect in the center of the cell by a basal ring of feces or pollen (Figs. 11, 12). The tubular-shaped fecal pellets were yellowish and were deposited in short strands, but in layers, on the upper $\frac{2}{3}$ of the walls and beneath the cell cap. The egg chamber (0.5 mm wide and 2 mm long) was located 40% of the way up the side wall and perpendicular to the cell walls (Figs. 13, 14). There was no evidence that the larvae deposited any silk. Hurd and Linsley (1959) reported that adults of *T. helianthi* entered nests of *Melissodes composita* Tucker, but they did not find any parasitized host cells.

One cell contained the coarctate prepupal larva of the meloid beetle *Nemognatha*. Another two *Melissodes* cells contained castings of earthworms, which presumably were deposited in the cell before the bee larvae matured.

Observations of Adults

Seasonal occurrence.—Since sunflowers were planted at three different times, bloom was available for the entire season. We counted all bees on the flower heads at 0900, 1100, 1300 hr every Monday, Wednesday and Friday from 25 July to 4 September. Both male and female *M. agilis* were present on July 25 when bloom began. At this time their wing margins were entire and their body hairs were not worn, indicating recent emergence. Both sexes were abundant throughout the summer. The pattern of their seasonal occurrence suggests a single generation/year. Their abundance from week to week closely followed the abundance of sunflower bloom (Fig. 15).

Daily activities.—Males were recorded more frequently from flower heads than females (2.4♂/1.0♀). Initially, males were more abundant at 0900 hr than at any other time, but in late August and early September, when morning temperatures began to be quite cool, their abundance was similar in all count periods.

Males gathered on sunflower heads in sleeping aggregations of from 2 to 20 bees/head in late afternoon and during inclement weather. No observations were made to determine if they chose the same sleeping cluster or the same flower head each night. They clustered in partially opened heads under the large ray petals. (The heads had to be tilted back before the bees could be seen.)

Female *Melissodes* were most abundant on the flowers early in the day. For example, at 0900 hr twice as many females were present as at 1100 hr,

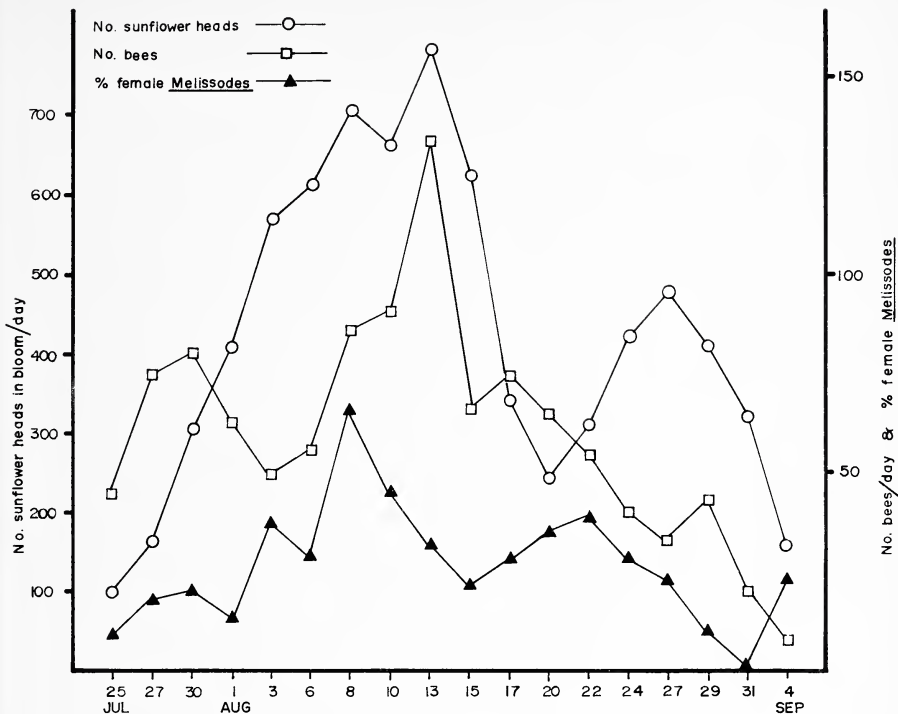


Fig. 15. Seasonal abundance of sunflower heads in bloom, number of *Melissodes*, and percentage of female *Melissodes*.

and at 1300 hr, about $\frac{1}{3}$ as many females were present as at 1100 hr. Apparently, most of the females remained in their nests in the afternoon; this was corroborated by observations of the activity of individual females at their nests (see below). Female *M. agilis* provisioned their nests exclusively with sunflower pollen. The maximum pollen load carried by a female bee was estimated at 330,000 grains (estimated by washing the pollen from the body hairs and counting the pollen grains with a haemocytometer) (Parker 1981b).

Triepeolus helianthi was present throughout the observation period. The activity pattern of this cuckoo bee varied with the time of day. In the morning, females were often observed flying slowly several inches above the soil and investigating all types of holes. Several were seen entering *Melissodes* nests where they remained only a few minutes (see below). In the afternoon, *Triepeolus* spent more time on the flowers than in the morning. Their abundance on flower heads at 1300 hr was nearly double that at 0900 hr. Thus, this parasite appears to search for and invade host nests primarily in the morning when most host adults are foraging and to forage in the afternoon when *Melissodes* remain in their nests.

Table 1. Mean time of foraging trips and within-nest periods of two *Melissodes agilis* females on three observation dates. Initial foraging trips for each day and extended within-nest periods (4, see text) excluded. Numbers in parentheses are standard deviation and sample size, respectively.

Observation date (August)	Mean time/foraging trip (sec)		Mean time within nest (sec)	
	S	M	S	M
2	231.5 (± 306.5 ; 10)	293.8 (± 225.6 ; 9)	43.3 (± 13.0 ; 9)	57.8 (± 11.8 ; 8)
7	501.1 (± 360.6 ; 11)	594.3 (± 408.1 ; 9)	65.6 (± 15.6 ; 10)	99.6 (± 83.5 ; 9)
13	950.5 (± 969.5 ; 11)	1,086.8 (± 715.0 ; 9)	84.8 (± 28.0 ; 11)	112.3 (± 90.3 ; 8)

Foraging Activity

We monitored the activity of two female *Melissodes* bees at the nesting site on three mornings, beginning at 0600 hr and using a stopwatch and portable tape recorder. The nests were within 50 cm of each other near the top of a furrow that separated a row of zucchini from the periphery of the planting. We recorded times for commencement of activity and the number and duration of trips from the nest as well as periods spent within the nest.

Both nests were unplugged and were without tumuli each morning when observations began. Bee activity commenced between 0630 and 0745 hr. Activity began earlier when temperatures were warm and cloud cover slight. Bee S always became active first and made her initial trips from the nest 5–15 minutes before bee M. The first trip was invariably an extended one for both bees; it varied from 21 to 32 minutes in duration. Most other trips were of shorter duration (Table 1). Bees returning from short trips invariably carried pollen. Bee S also consistently completed her foraging trips more rapidly than did bee M. Bees entered their respective nests from return flights without hesitation and never investigated each others' nests.

There was no discernible difference between the duration of early and later foraging trips for either bee on any date, as might be expected if pollen or nectar were becoming limiting later in the morning. However, foraging trips became longer as the month progressed for both bees. The relatively extended trips of 13 August were associated with sporadic rainfall and heavy cloud cover throughout the morning. Both bees were trapped in the field by rain on several occasions and did not return until the rain had ceased. Although cloud cover remained heavy, both bees left for additional foraging trips after brief periods in the nest.

Periods spent within the nest after the bees returned from foraging trips were usually short (30–150 sec); presumably the pollen and nectar that the bees had collected were deposited during these brief periods in the nest. Occasionally, within-nest periods were much longer; four such periods ranging from 21 to 41 minutes were recorded. We believe that pollen loaf prep-

aration, egg laying and cell closure occurred during these extended within-nest periods. If this is so, then the number of foraging trips necessary to provision a single cell can be estimated from the ratio of short/long within-nest periods. For the two bees, we recorded 55 short and 4 long periods, for an estimate of approximately 14 foraging trips/cell.

On the first two dates, we terminated observations at 1000 hr, when the bees had been in their nests for at least 30 consecutive minutes. Foraging appeared to cease on both days by approximately 0915 hr. By this time, bee S had made 11 trips on 2 August and 12 on 7 August; bee M had made 10 trips on each day. Subsequent foraging activity was minimal, as previously shown by comparisons of numbers of females recorded on flowers at the different time periods. An exception was on 13 August, when the bees foraged in sporadic rain until just after 1100 hr. Although we continued observations until 1200 hr, neither bee emerged again. It is interesting to note that at 1100 hr, bee S returned from her 12th trip and M returned from her 10th trip, the same number as had been made on previous days.

We observed a single intrusion by *Triepeolus helianthi* into the nest of bee S on 2 August. The cuckoo bee was first seen flying around the nesting site at 0755 hr, while both *Melissodes* were active. The *Triepeolus* remained in the vicinity resting on the ground or on nearby vegetation. At 0803 hr, she briefly investigated the entrance of S's nest while the latter was out and then moved to about 10 cm west of the entrance. S returned, remained in the nest for a brief period, and left at 0807 hr. As S was leaving, *Triepeolus* began to move towards the entrance and entered less than one second after S had left. *Triepeolus* remained in the nest for 90 sec, then crawled out and down the furrow. She then flew to a nearby grass blade, where she remained, pulsated her abdomen for several seconds and then left. When the nest was excavated in September, two larvae of *Triepeolus* were found.

Discussion

This study and those of Parker (1981a, b) have shown that *Melissodes agilis* possesses numerous characteristics which make it a valuable pollinator in commercial sunflower plantings. The emergence of *M. agilis* adults was closely synchronized with the initiation of sunflower bloom, and numbers of bees followed the number of flowers available (Fig. 15). Females exclusively used sunflower pollen to provision their cells (Parker 1981b). In contrast to some other species of anthophorid bees in which the nesting site is patrolled by males in their search for females (e.g. *Centris*, Alcock et al. 1977), male *M. agilis* patrol the flowers for prospective mates. Thus, both sexes are important pollinators. Finally, because females nested in or adjacent to the planting, foraging trips were of short duration, and females were probably able to complete approximately 1 cell/day. Elsewhere (Parker

1981a, b) has shown that *M. agilis* is also a more efficient pollinator than the commonly used honey bee. Indeed, although the honey bee is usually credited for most sunflower pollination (McGregor 1976), natural field populations of *M. agilis*, which are usually ignored, may be more important.

The tendency of *M. agilis* to nest in sunflower fields makes their populations vulnerable to certain tillage practices. Since cells were constructed at soil depths between 11 and 19 cm, tillage practices that disrupt the soil below 10 cm are likely to have a devastating effect on populations of *M. agilis*. A zero or minimum tillage system (Robinson 1978), where appropriate, would be least hazardous to *Melissodes* populations.

Acknowledgments

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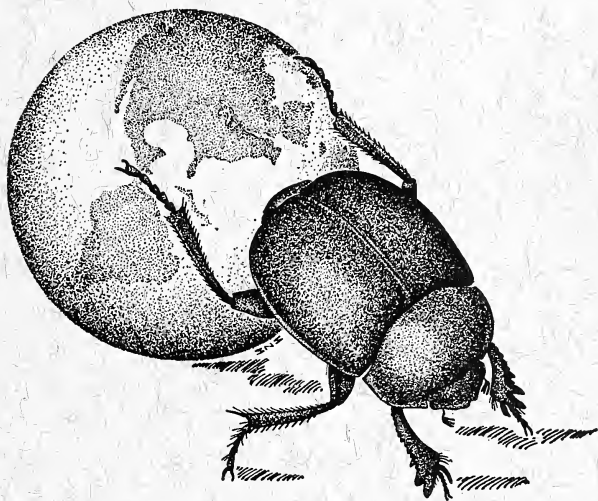
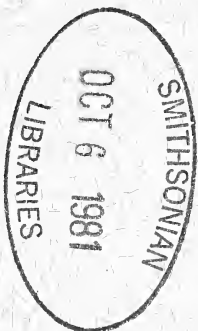
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EDWIN WAY TEALE 1899-1980

Alexander B. Klots

Edwin Way Teale, one of the oldest and most distinguished members of the New York and Brooklyn Entomological Societies, died in Norwich, Connecticut on 18 October, 1980. A member of each society since the 1930's, he received the John Burroughs Medal and a Pulitzer Prize for his natural history writings. He served as President of the New York Society in 1944 and President of the Brooklyn Society in 1950-51 and 1953-54.

Born in Joliet, Illinois in 1899, Mr. Teale attended Earlham College in Indiana (where he met his wife, then Nellie Donovan) and later Columbia University. During his career Nellie, herself a keen and devoted naturalist, was always with him. Perhaps she specialized on plants more than Ed did, but together they made an ever-close team for the observation and understanding of nature.

The Teales soon came to New York, where Ed became a staff writer for Popular Science magazine and "free-lanced" for some years. Eventually he wrote his first book, *Grassroot Jungles* (1937) and from then on concentrated on photography and writing books, and never looked back. Eventually he published more than 20 books "of his own" in addition to scholarly and sensitive studies of the lives and works of such great naturalists as Thoreau, Hudson, Audubon, Fabre, Burroughs and Muir.

Many of the Teale books show a marked preoccupation with seasonal changes. His most famous series: *North With The Spring*, *Journey Into Summer*, *Autumn Across America* and *Wandering Through Winter* tells of how the Teales followed the changing seasons throughout the United States and Canada. It was for this series that he received the Pulitzer Prize in 1966.

Entomology played a very large part in the Teale writings, much more so than in those of other authors. Even as a boy he was fascinated by the complexity of the lives of insects; and this continued throughout his life. *A Book About Bees* (1940), originally titled *The Golden Throng*, is a very thorough description of the complexity of life in a honeybee hive. Like his other books it was illustrated with his own photographs.

Photography indeed played a very large part in Teale's life. Starting with what today seems a crude and cumbersome apparatus, a big bellows-extension camera and a loose flash-powder gun, Teale constantly photographed his subjects. His photographs covered all phases of nature; and many of them are superb by any standards.

Living in Baldwin, Long Island, Teale could be a faithful attendant at meetings of the two entomological societies, and constantly showed up with an interesting note on some observation, or a remarkable photograph. Many of his observations were real contributions to knowledge. Then, in 1959,

encroaching urbanization dictated a move. Partly on this writer's suggestion a large area with a very old house was bought in largely rural Hampton, Windham County, Connecticut. "Trail Wood," as the place was christened, is almost ideal for the naturalist, with many acres of unsullied old and young woodlands, fields, pastures, hillsides, a beaver pond, a brook and, a recent addition, a large, clear pond. Here for many years Ed and Nellie came to know the most intimate details of the ever-abundant, ever-changing wildlife.

Despite his great familiarity with all phases of natural history Ed never wavered in his primary interest in insects and their ways. After the move to Connecticut he usually managed to have business affairs and conferences with his publishers in New York scheduled for Tuesdays so that he could attend the dinners and meetings of the New York Entomological Society. He always arrived with some new and interesting observation to tell about.

I particularly remember once when Ed and I were watching and photographing close-up a large bullfrog floating just below the surface at the edge of his pond. Ed noticed and commented on the fact that the frog kept only one eyeball at a time above the surface. The above-water eye would be pulled down as the other came up in irregular sequence. How delighted he was when we noticed that tiny biting midges, or "no-see-ums" (*Ceratopogonidae*) were feeding on the protruding eyeballs. When one was pulled down they simply shifted to the other as it came up. We later learned that there are species that specialize on amphibians! With the insects, always something new!

"Trail Wood" will be taken over and maintained as the Edwin Way Teale Memorial Sanctuary (and nature center) by the Connecticut Audubon Society when Nellie no longer wishes to live there. Ed's manuscripts and books will go to the Library of the University of Connecticut at Storrs and be maintained there in a special memorial section.

HYDROPSYCHE LARVAE (TRICHOPTERA: HYDROPSYCHIDAE)
FROM A LAKE WEEDBED

Bernard A. Marcus¹

Abstract.—In February of 1979, two individual larvae of *Hydropsyche* sp. (Trichoptera: Hydropsychidae) were collected from submerged aquatic plants in Conesus Lake, N.Y. at 1.8 m in depth where they may have survived for as long as ten months. No previous report on these organisms suggests that they occur in such a situation. It is possible that their absence from lake weed beds is due to factors other than simply unfavorable environment.

Published information on the larvae of hydropsychid caddisflies (Trichoptera) generalizes that these organisms are commonly found in lotic waters where they spin nets on the substrate and capture food materials that are carried by the current (Denning 1968; Hynes 1970; MacKay 1978). In Great Britain, hydropsychid larvae are found only in rivers and streams, not in lakes or ponds (Eddington 1968).

In North America, hydropsychid larvae are found in the wave-washed shoreline areas of large lakes. Barton and Hynes (1978) specified that they can manage in standing water if there is sufficient movement to deliver food materials to their nets. These investigators collected specimens from the exposed Canadian shores of the Great Lakes. Much earlier, Ross (1944) reported finding *Hydropsyche recurvata* Banks larvae along the Illinois shore of Lake Michigan, at Evanston, living among the rocks in less than one meter of water. Wiggins (1977) reported finding the same species, along with larvae of the genus *Cheumatopsyche*, along the shore of Lake Winnipegosis in Manitoba, Canada.

On February 19, 1979, I captured two larvae of *Hydropsyche* sp. from a bed of submerged aquatic macrophytes at the Dacula Shores (inlet) area of Conesus Lake, New York. The organisms were found among a sample containing 75% *Heteranthera dubia* (Jacq.) MacM.; 20% *Ceratophyllum demersum* L.; and 5% *Elodea canadensis* Michx. The plants, growing in 1.8 m of water, were collected through the ice by means of a rake. Both larvae appeared to be later instars. To my knowledge, this is the first time these organisms have been reported from such conditions. Between January and August, 1979, monthly collections were made at weedbeds at five separate

¹ Present address: Division of Mathematics and Science, Genesee Community College, Batavia, New York 14020.

sites on Conesus Lake at depths from 1.5 to 4.0 m. Similar collections were taken from six sites at nearby Honeoye Lake at depths from 2.0 to 3.0 m. *Hydropsyche* larvae were found only in the February 19 collection at 1.8 m at Dacula Shores in Conesus Lake. The general absence of the larvae from the lake vegetation is consistent with the knowledge on the family; the single find is an unusual, but still interesting, event.

Dacula Shores is in the southernmost part of Conesus Lake. Conesus Inlet, the lake's major tributary, empties into this area. Although the inlet is the principal contributor of water to the lake (Forest, Wade and Maxwell 1978), it is sluggish near its mouth and does not appear to offer the type of habitat preferred by Hydropsychidae. Additionally, any hydropsychid larvae among the invertebrate drift (Waters 1965) from the inlet would have ample opportunity to settle in the mouth of the stream well before even entering the lake. Furthermore, the sampling site at Dacula Shores is beyond the zone affected by water movement from the inlet.

The most plausible explanation, then, for the occurrence of typically running water invertebrates in a lake weedbed is that they were carried in from the inlet stream during an episode of unusually high water. Organisms usually do not survive that experience for very long (Dendy 1944). If this is the case, however, the two larvae collected would have survived for up to ten months in the lake environment, to which they are supposedly poorly adapted. The previous high waters would have been in the Spring of 1978.

While one case does not refute the general rule on the ecology of immature hydropsychids, it does offer an interesting note on their survivability, and suggests that similar possibilities should not be overlooked in field studies. If survival under these conditions is more common than previously known, then the absence of hydropsychid larvae from the submerged weedbeds of lakes may be attributed to reasons other than their simple inability to tolerate that kind of environment.

Acknowledgments

I am indebted to Dr. Herman S. Forest, State University College at Geneseo, N.Y. for his criticisms of the manuscript and to an anonymous reviewer for pertinent references.

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Environmental Resource Center, State University of New York College of Arts and Science, Geneseo, New York 14454.

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THE LARVA OF *AGROTIS VOLUBILIS* HARVEY
(LEPIDOPTERA: NOCTUIDAE)¹

Timothy L. McCabe

Abstract.—The mature larva of *Agrotis volubilis* Harvey (Lepidoptera: Noctuidae) is described and illustrated. *Achillea millefolium* L. was found to be an acceptable host. Late instar larvae became more general, accepting *Vaccinium vacillans* Torr. and *Oenothera biennis* L. Larvae were full-grown by the 20th of July (52 days), but would not pupate. They remained healthy through October, when they were placed in out-of-door cages; the larvae failed to overwinter.

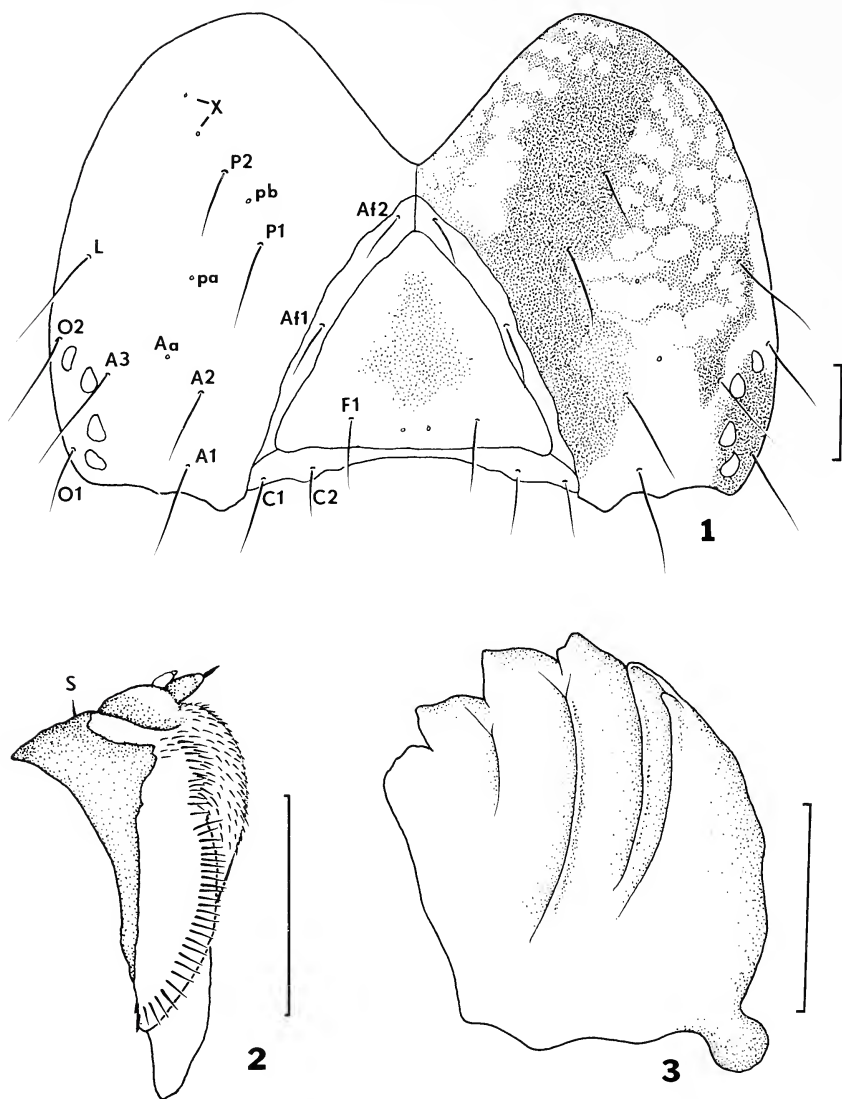
Despite the economic significance of the genus *Agrotis*, many species' biologies are unknown and identification of the adults of several species is hampered by the paucity of species-specific genitalic characters and the variability shown in adult habitus. *Agrotis volubilis* Harvey (1874) can not presently be satisfactorily separated from *A. stigmosa* Morrison (1874) or even *Feltia* [*Agrotis*] *musa* Smith (1910) on the basis of adult morphology (Ahmadi, 1977).

The genitalia of the *A. volubilis* parental female, whose progeny form the basis of this paper, has posterior apophyses which extend to the base of the anterior apophysis, as in Ahmadi's (1977) illustration of *A. stigmosa*; his specimen was from North Dakota. I have seen paratypes of *A. stigmosa*, described from Massachusetts, and these may represent a very pale form of *A. volubilis*, but it seems likely that it is a valid coastal species. The parental female, from the Pine Bush, Albany County, New York, resembles the inland and not the coastal species in habitus and I have called it *A. volubilis*. It compares well with Holland's (1903) figure of *Feltia* [*Agrotis*] *volubilis*.

The only biological information on *A. volubilis* is a paper by Hawkins (1930). This is a table of ratios of the tarsal claw of various noctuids. No information is available on the larva of *A. musa* or *A. stigmosa*.

A female *A. volubilis* was collected on May 28th, 1978, and ova were obtained by the 30th. The first instar larvae were confined with *Taraxacum officinale* L., *Prunus virginiana* L., *Achillea millefolium* L., and *Populus tremuloides* Michx., but fed only upon the *Achillea*. Later instar larvae would feed on *Vaccinium vacillans* Torr., and *Oenothera biennis* L., but

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Figs. 1-3. *Agrotis volubilis*, Pine Bush, Albany Co., New York: 1, frontal aspect of head; 2, hypopharyngeal complex; 3, oval aspect of left mandible. Scale lines equal 0.5 mm.

only sparingly on the latter. All larvae were ultimate instars by 20 July. At this point there was a marked decrease in feeding and the larvae crawled beneath the litter at the bottom of the rearing tray and fed only enough to maintain fluids and weight. This torpid state lasted through the remainder of the summer and fall and on 20 October 100 larvae that had not been

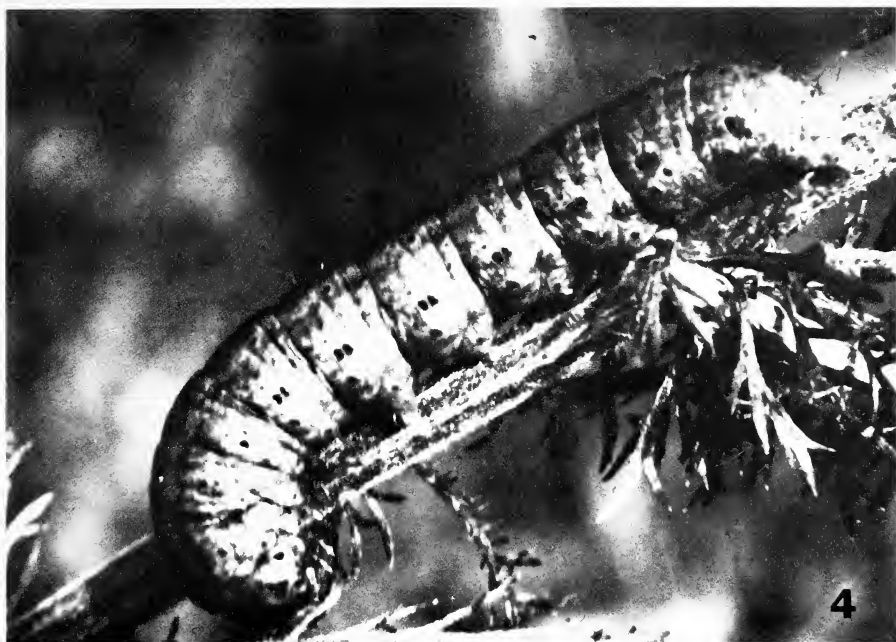
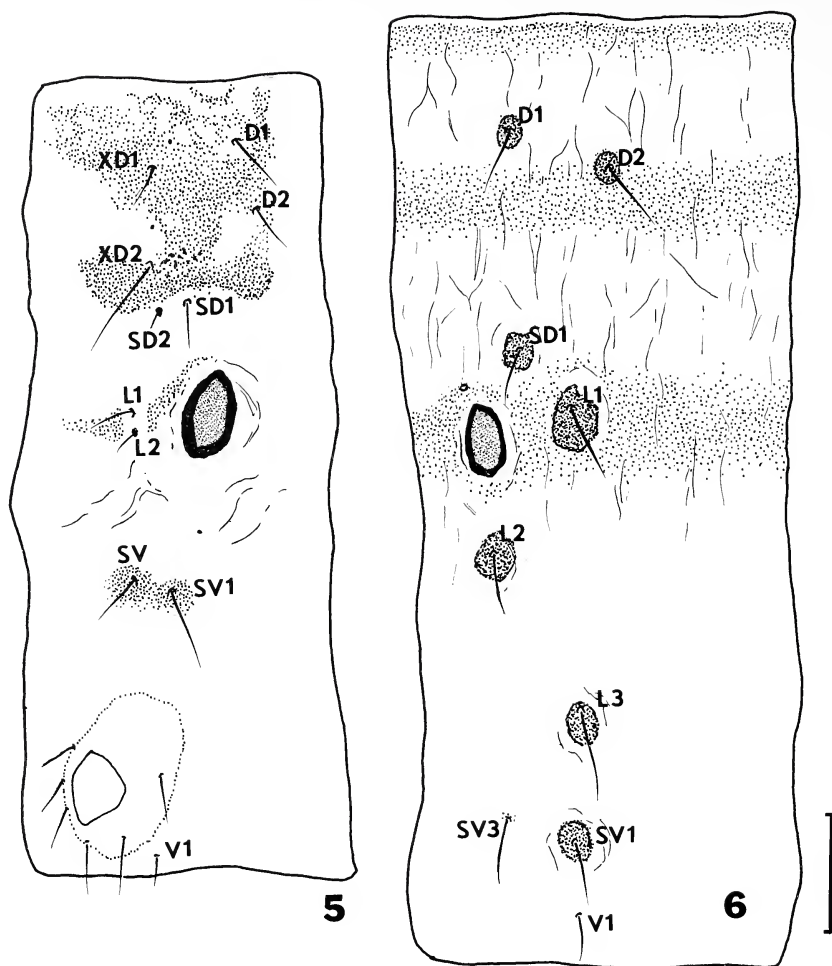


Fig. 4. *Agrotis volubilis*, Pine Bush, Albany Co., New York: photograph of living, sixth instar larva.

preserved were left in out-of-door cages. The larvae did not survive the winter.

Larvae were reared in continuous darkness, interrupted by addition of fresh leaves every two days. This procedure usually causes larvae to bypass a diapause, and, with night feeding larvae, accelerates development. Apparently this species has a summer aestivation followed by an obligatory larval diapause to overwinter. This is supported by the spring appearance of adults and univoltinism in nature throughout its range. Crumb (1929) reported similar adaptive strategies in species of *Feltia* and in another *Agrotis* species.

Agrotis venerabilis Walker (1856) and *A. volubilis* larvae are extremely similar and no consistent larval mouthparts or head capsule differences were found. The size and relation of the Abl L1 pinaculum to the Abl spiracle seem to offer reliable differentiating characters: the pinaculum and the spiracle are the same size in *A. volubilis*, that of *A. venerabilis* have the pinaculum 50% larger than the spiracle; the spiracle of *A. volubilis* is 0.52 mm high, that of *A. venerabilis* is 0.36 mm high on average (the full grown length is comparable in the larvae). Considering the above similarity in two



Figs. 5-6. *Agrotis volubilis*, Pine Bush, Albany Co., New York: 5, prothorax; 6, first abdominal segment. Scale line equals 1.0 mm.

"distant" *Agrotis* species, it may not be possible to distinguish *A. musa*, *A. stigmata*, and *A. volubilis* larvae.

Larval setal nomenclature follows Hinton (1946) with the exception of the ultraposterior coronal punctures which are labelled with an X.

First Instar Larva.—First instar larva with primary body setae tipped with a knob; proleg Ab3 rudimentary, Ab4 one-half the size of Ab5; proleg Ab5, Ab6, and Ab10 all well developed.

Sixth Instar Larva.—General (Fig. 4): Average head width 3.20 mm; average total length (fully extended) 42.0 mm; abdominal prolegs present on

3rd through 6th and 10th segments; setae simple; crochets a uniordinal mesoseries; spiracle A8 0.50 mm high on average ($N = 18$).

Coloration (living material): Head (Fig. 1) with a brown, oblique band from vertex and then expanding ventrally to encompass entire adfrontal line; reticulate pattern present dorsal to band and between band and stemmata. Body gray-brown with conspicuous lateral series of black spots, two on each segment comprising the spiracle and the 1st lateral (L1) pinaculum.

Head (Fig. 1): Epicranial suture 0.50 mm long; height of frons 1.03 mm. Second adfrontal (Af2) anterior and 1st adfrontal (Af1) posterior to apex of frons. Coronal punctures Aa, pa, pb, and 3 ultraposterior (2 visible in frontal aspect) present as illustrated.

Mouthparts: Hypopharyngeal complex (Fig. 2): spinneret shorter than labial palpus, apex lacking setae; stipular seta (S) at anterodorsal region of prementum; distal region of hypopharynx bears numerous fine spines, followed by a single row of 25–30 spines which extends to the posterior apex of the prementum. Mandible (Fig. 3) with inner ridges distinct, lacking basal tooth. Sixth outer tooth low, divided into smaller subteeth.

Thoracic segments: Prothorax (Fig. 5): cervical shield weakly sclerotized. Subdorsal setae (SD1 & SD2) lacking pinaculi; prespiracular setae (L1 & L2) also lacking pinaculi. Subventral setae share common pinaculum. Meso- and metathorax with dorsal and subdorsal setae (D1, D2, SD2, and SD1) all in a vertical line through center of segment and each on its own pinaculum; SD1 peculiarly modified, surrounded by an inverted horseshoe-shaped pinaculum and with a very large, black setal base which is twice the diameter of other setal bases although the seta itself is less than half the size of other primary setae. Angle of L3-L1-L2 120° .

Abdominal segments: Ab1 (Fig. 6): two subventral setae (SV1 & SV3); L1 posterior to spiracle; SD2 seta reduced or absent, but setal base always present anterodorsal to spiracle, rarely contiguous with upper margin of spiracle; spiracle 0.52 mm high. Ab2–6 with 3 subventral setae; SD2 setal base anterior to spiracle. Ab7&8 with only 1 seta in subventral group.

Crochets a uniordinal mesoseries: 9–15 on Ab3 (mode = 12), 12–19 (15) on Ab4, 13–20 (16) on Ab5, 14–18 (17) on Ab6, and 17–23 (20) on Ab10. Material examined. Eighteen specimens, Pine Bush, lat. $42^\circ 34' 07''$, long. $73^\circ 52' 53''$, Albany County, New York, elev. 91 meters, 30 July 1978, from ova of female collected and determined by T. L. McCabe. Pl♀ and all larvae are coded tlm 78–65.

Acknowledgments

I thank Linnea Johnson for the illustrations. Voucher specimens of the larvae will be deposited in the New York State Museum and the United States National Museum.

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New York State Museum, The State Education Department, Cultural Education Center, Albany, New York 12230.

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HISTOLOGICAL CHANGES IN THE ANTENNA OF *TENEBRIO*
MOLITOR L. AFTER IMAGINAL ECLOSION
(COLEOPTERA: TENEBRIONIDAE)

Louis D. Trombetta and James Forbes

Abstract.—The histology of the antenna of *T. molitor* and the changes which take place in its maturation from imaginal eclosion to one week of age are compared. The cuticle, epidermis, nerves and tracheae are described. A mesocuticle is present in the cuticle, and a blood vessel is described for the first time in the antenna of a beetle. In the one week old insect the endocuticle becomes thicker, the underlying epithelial cells lower in height, the layer of nerve fibers beneath the epithelium more compact, and the walls of the tracheal trunks and blood vessel thinner.

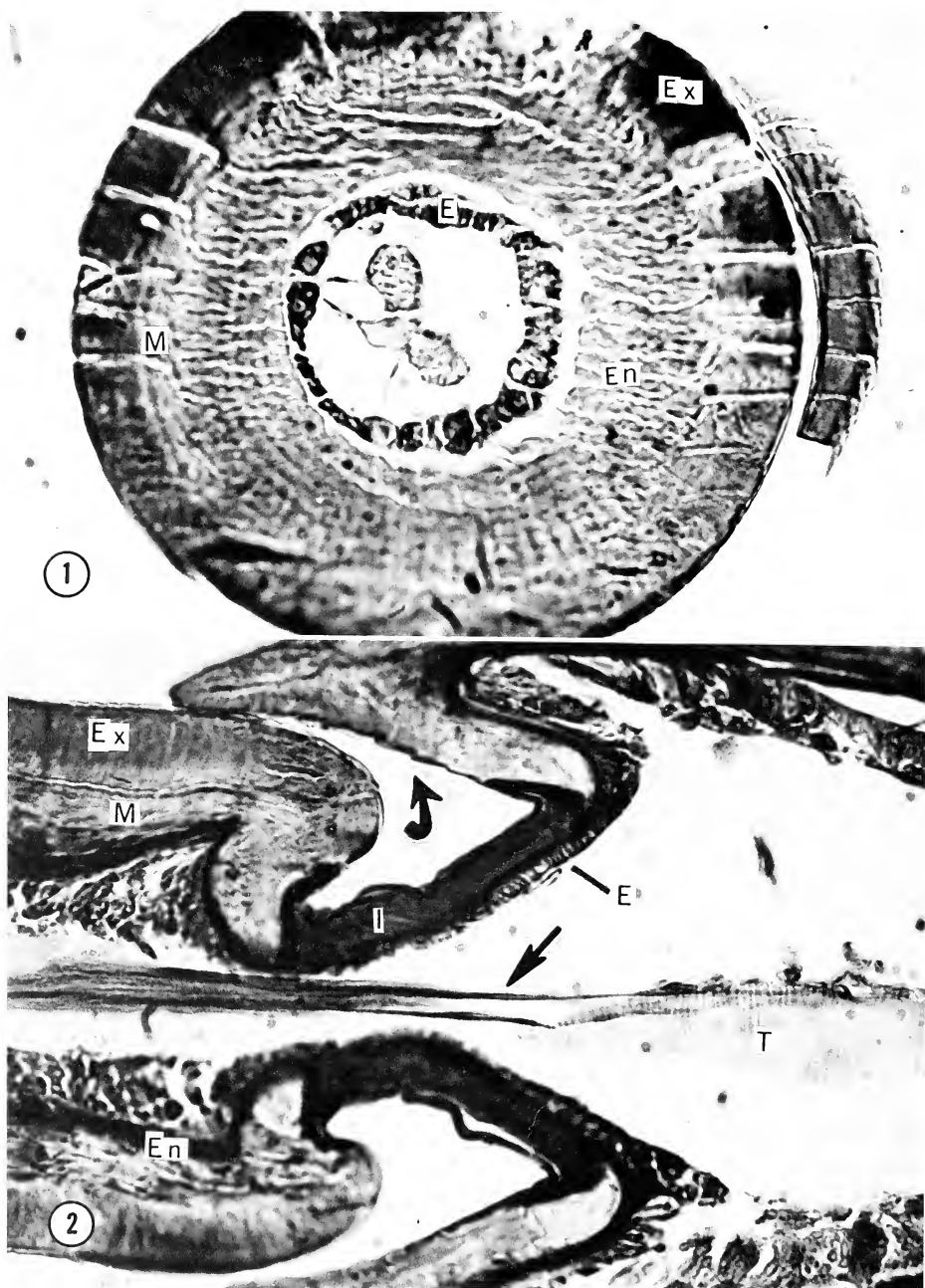
Only two studies include observations on the anatomy of the coleopteran antenna: Borden (1968) on the antennae of the scolytid *Ips confusus* and Chang and Jensen (1973) on the curculionid *Rhabdocelus obscurus*. Most investigations of this organ have concentrated on the morphology and physiology of its sensilla (Roth and Willis 1951; Slifer and Sekhon 1964; Moeck 1968; Ernst 1969; and Borg and Morris 1971). The sensory receptors of *T. molitor* have been studied by Valentine (1931), Pielou (1940), Doyen (1966), Pierantoni (1974), and Harbach and Larsen (1977a, b).

This paper is the first description of the histology of the antenna of *T. molitor* and describes the changes which take place during the first week after imaginal eclosion.

Newly emerged and one week old adults were removed from individual cultures and immediately placed in alcoholic Bouin's solution where the antennae with their musculature were removed. After fixation for 12 hours, they were washed and stored in 80% ethyl alcohol. The antennae were processed and sectioned by a technique previously described (Trombetta and Forbes 1977). The sections were stained with Harris' haematoxylin counterstained with eosin Y, Sharp's modification of Mallory's triple stain (Kennedy 1932), safranin counterstained with fast green, and an argentaffin staining technique (Lillie 1954).

Observations

One week old adult. The antenna of *T. molitor* is moniliform in shape and consists of the scape, the pedicel, and a flagellum that has nine subsegments or annuli joined to each other by membranes. These annuli give the flagellum



Abbreviations: BV—blood vessel, E—epidermis, En—endocuticle, Ex—exocuticle, I—intersegmental membrane, J—sensillum of Johnston's organ, M—mesocuticle, N—nerve trunk, S—sense cell, Sn—sensory receptor, T—trachea.

a segmented appearance, but, because they do not contain muscles, are not true segments (Schneider 1964). Longitudinal sections of the antennae show a segmental arrangement of the annuli, and in recording the observations the older description of the antenna, that it consists of 11 segments, is used. The procuticle of the adult antenna consists of three layers: the exocuticle, the mesocuticle and the endocuticle (Fig. 1). The exocuticle is heavily sclerotized, and in sections it is amber in color and does not readily stain. The thickness of this layer varies in each segment from $23\ \mu$ at the base to $17\ \mu$ at its terminal end. The only exception to this is in the distal segments where because of the numerous sensory receptors it can be as thin as $9\ \mu$. In the intersegmental regions the proximal segment forms a depressed ring into which the base of the next distal segment fits. On the inner surface of the ring, the exterior of the exocuticle is serrated (Fig. 2).

A mesocuticle is present beneath the exocuticle from the scape to segment ten. This layer varies in thickness, stains with safranin and eosin, and except for some red blotches does not stain with Mallory's stain (Figs. 1 and 2). No mesocuticle is seen in the eleventh segment.

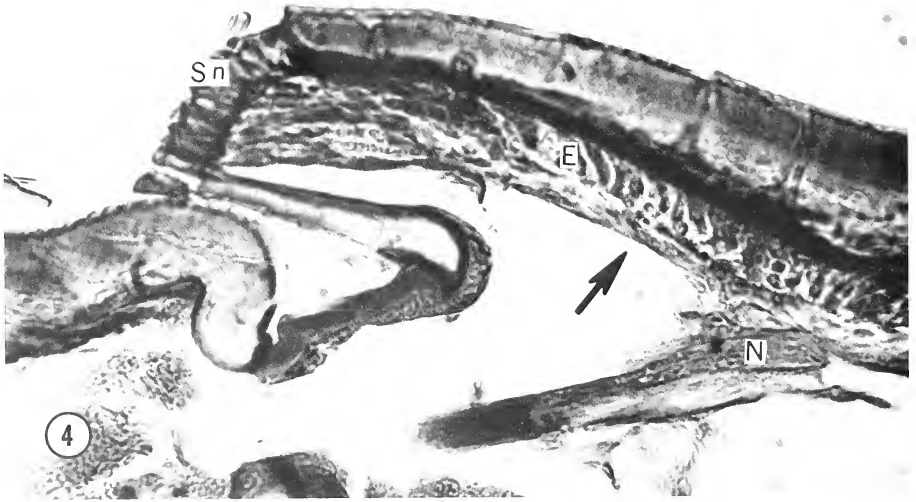
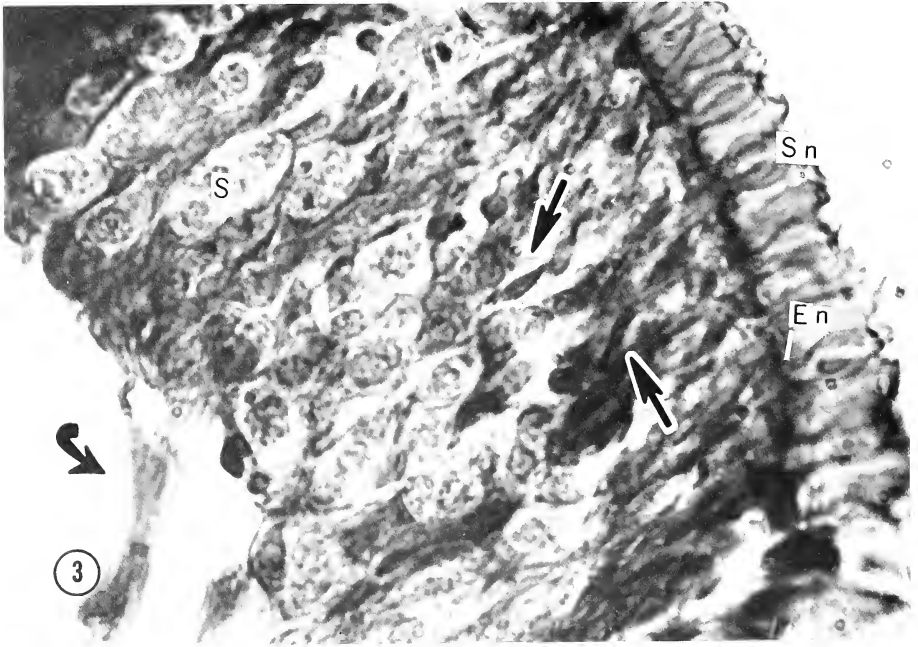
The endocuticle lies beneath the mesocuticle, except in the eleventh segment where it lies directly beneath the exocuticle. It stains lightly with haematoxylin and with fast green and red with Mallory's stain. This layer is laminated and is thickest at the bases of segments six to eleven (Fig. 1). Here as many as ten lamellae are visible, and it is twice as thick as the exocuticle. In the remaining segments the thickness of the endocuticle varies, but generally it is thickest in the center of the segment and is thinnest at the articulatory regions; slightly thicker at the proximal than at the distal. Where numerous sensory receptors are located, the endocuticle appears as a very thin layer, about $3\ \mu$ in thickness (Fig. 3). In other regions the dendrites of nerves traverse the thick endocuticle to innervate receptors. In the scape the endocuticle is thin and never exceeds five lamellae in thickness.

Pore canals appear under the oil immersion lens as very fine striations extending through the endo-, meso-, and exocuticle. When stained with the argentaffin staining technique, they appear tubular in structure, and are straight, not helical, and end in a small bulb beneath the epicuticle.

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Fig. 1. Cross section of a one week old adult antenna showing the arrangement of the cuticular layers and the epidermis. Haematoxylin and eosin. $\times 400$.

Fig. 2. Longitudinal section through the intersegmental membrane between two antennal segments of a one week old adult antenna. The endocuticle appears dark because it is stained red with Mallory's. Note the serrated edge on the depressed ring of the proximal segment (curved arrow). The blood vessel appears as a smooth-surfaced tube (straight arrow). Mallory's stain. $\times 400$.



The intersegmental membrane between the antennal segments is a thin, unsclerotized membrane, which appears white in color when unstained (Fig. 2). It stains with fast green and appears as a single layer continuous with the endocuticle of the adjoining segments. Mallory's stains two layers of the intersegmental membrane, an exterior layer which stains red and the interior layer which stains blue. In some of these intersegmental membranes random areas of the interior layer have an amber color not unlike that of the exocuticle.

The epidermis underlying the cuticle is composed of a simple epithelium (Fig. 1) that varies from columnar to squamous depending on location and density of the nervous tissue. In the proximal segments, where the sensory receptors and the underlying nerve fibers are not numerous, the cells are cuboidal or columnar. In the distal segments where these nervous elements are numerous the cells are lower in height and are scattered among the sensory cells. At the bases of the distal segments the cells are cuboidal and appear small in comparison to the overlying cuticle. In the intersegmental membranes the cells are also cuboidal. These epidermal cells have a large, centrally located nucleus with peripheral chromatin, and their cytoplasm is extremely basophilic in staining reaction. These cells stain strongly with safranin and with Mallory's stain they appear brown yellow in the proximal segments but brown red in the distal.

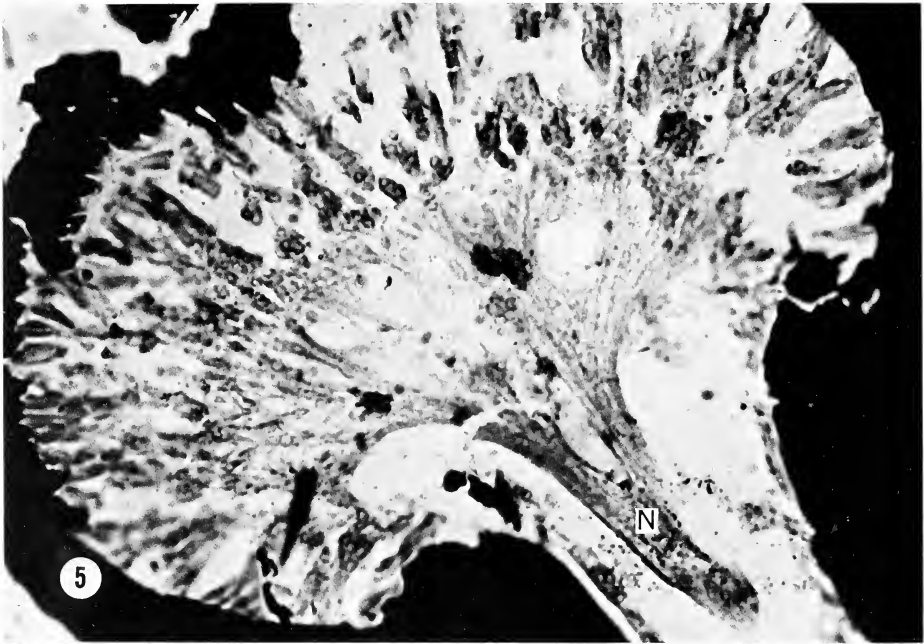
In some regions of the antenna, between the epidermal cells and the endocuticle a very thin, blue green layer can be seen in sections stained with Mallory's stain. Beneath the epidermis the basement membrane is seen as a fine, blue green layer when stained with Mallory's stain. However, when nerve fibers and fine tracheae underlie the epidermal cells, the basement membrane is not evident.

The sensory cells of the adult antenna are typical for insects. They have short, distal dendrites and long axons that join to form large branches. The axons and dendrites stain with fast green and stain light blue with Mallory's stain. The cytoplasm of the cell body of these cells stains deep red with safranin and blue with Mallory's stain. The nucleus stains darker than the cytoplasm and contains peripheral chromatin. Sensory cells of the receptors are found either singly or in clusters (Figs. 3, 4) throughout the antenna.

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Fig. 3. Cross section through numerous sensory receptors in a distal segment of a one week old adult antenna. Note the elongated and scattered epidermal cells (straight arrows) and a nerve branching to the sense cells (curved arrow). The endocuticle appears as a thin layer. Mallory's stain. $\times 1,000$.

Fig. 4. Longitudinal section through a distal segment of a one week old adult antenna showing a branch of the nerve trunk (straight arrow) extending toward an aggregation of sensory receptors. Mallory's stain. $\times 400$.



A large antennal nerve extends from the deutocerebrum of the brain to the antenna. In the scape it innervates the intrinsic antennal muscles and then divides to form two nerve trunks that extend up the antenna and end in terminal arborizations in the eleventh segment. These nerve trunks give off many fine branches which innervate the solitary sensory receptors, while they extend up toward the distal segments. In these distal segments where there are aggregations of sensory receptors, larger nerve branches split from the antennal nerve trunks and innervate them (Figs. 4, 5). Each nerve trunk is surrounded by a thin nerve sheath with flat nuclei (Fig. 6). Sections of the nerve trunks show an intense safranin staining central area, that stains darker than the peripheral nerve sheath nuclei.

Johnston's organ can be seen in cross sections of the pedicel as clusters of sensory cells encircling the nerve trunks, the blood vessel and the tracheae (Fig. 7). These clusters of sensory cells are attached by their axons to branches of the nerve trunks, and their dendrites extend into the inter-segmental membrane between the pedicel and third segment (Fig. 8).

The nervous tissue in the antenna of the one week old adult is associated with the epidermis in three ways. First, sensory cells may lie next to epidermal cells with their axonal fibers extending to an antennal nerve branch as in the case of a solitary receptor or a small aggregation of receptors (Fig. 3). Second, a nervous layer lies immediately beneath the epidermal cells. This layer consists of nerve branches extending from the nerve trunks and from which dendrites extend to the receptors (Fig. 4). Third, nerves have almost completely displaced the epidermal cells as in the eleventh segment.

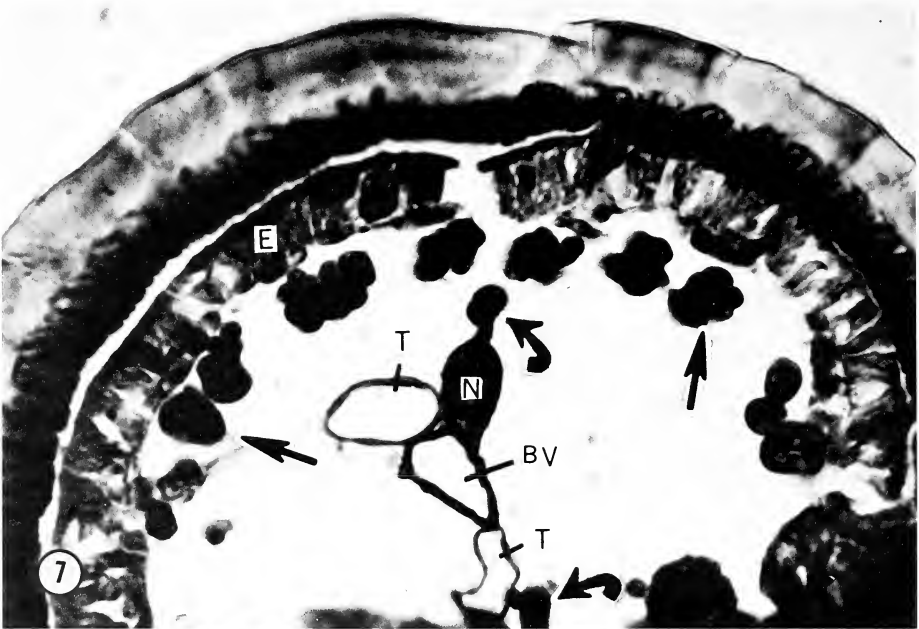
A large trachea enters the antenna, and in the third segment it bifurcates. These two tracheae course through the lumen of the antenna and send tracheoles to the epidermal cells and to the sensory cells (Figs. 6, 7). The tracheoles are extremely numerous in regions where there are numerous receptors. They vary in size and some of the smallest lie against the basement membrane of the epidermis. They give the appearance of being rigid and circular in shape or collapsed. The tracheae are composed of extremely thin cells with few nuclei and these protrude into the antennal lumen. Internal to this epidermal lining a very thin cuticle with taenidia surrounds the tracheal lumen (Figs. 2, 6).

The blood vessel is found among the nerve trunks and tracheae and extends straight through the antenna with no branches. It is always closely

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Fig. 5. Oblique section through the last antennal segment of a one week old adult antenna showing the arborization of an antennal nerve. Argentaffin stain. $\times 80$.

Fig. 6. High power view of a cross section of a one week old adult antenna showing the arrangement of nerve trunks, tracheae and blood vessel. Arrows indicate the nuclei of the nerve sheath and tracheae. Haematoxylin and eosin. $\times 1,400$.



associated with one of the nerve trunks and usually lies directly against it. The diameter of the blood vessel varies throughout the antenna, but it is always largest in the third segment. No pores or openings in the vessel were seen, not even at the tip. The wall of the blood vessel has many nuclei and generally appears thicker than that of the tracheae.

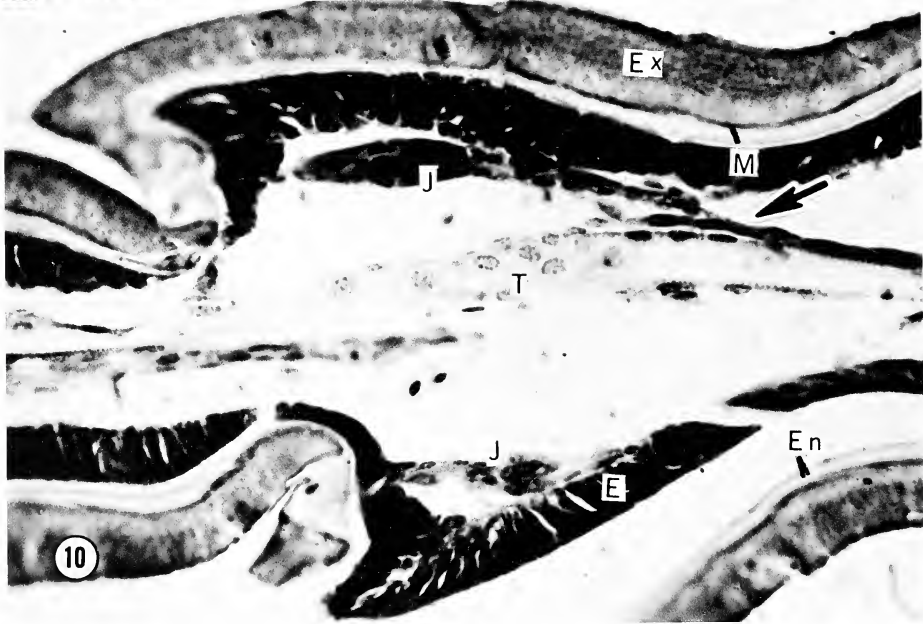
Newly emerged adult.—The antenna of the newly emerged adult is not heavily sclerotized. The exocuticle ranges in thickness from $23\ \mu$ at the bases of the antennal segments to $17\ \mu$ in the terminal regions of the proximal segments and $14\ \mu$ in the terminal regions of the distal segments. This layer is similar to that of the one week old adult in that it is thinnest where there are aggregations of sensory receptors. In unstained sections its color is light yellow in the proximal segments and amber in the distal regions (Figs. 9, 10). Only when the antenna is stained with Mallory's stain can light red blotches be seen in the exocuticle. The mesocuticle appears as a very thin layer throughout the antenna when stained with safranin and eosin but not with Mallory's stain (Figs. 9, 10). The endocuticle ranges in thickness from $2\ \mu$ to $3\ \mu$. It is thickest at the bases of the segments as well as in the terminal regions of the proximal segments. It is present as a very thin layer in areas of the antenna where there are aggregates of sensory receptors. It stains with haematoxylin, fast green, and red with Mallory's stain. Where epidermal cells have pulled away from the endocuticle in sections of the newly emerged adult, its inner edge is highly irregular but fits into the surface contours of these cells. When this artifact is seen in sections of the one week old adult beetle, the inner edge of the endocuticle is relatively smooth. The pore canals are present and are similar in arrangement and position to those in the cuticle of the one week old adult beetle.

The cuticle of the intersegmental membrane is thinner than that of the segments and consists of two layers. The inner layer, $10\ \mu$ thick, stains blue with Mallory's stain while the outer, only $3\ \mu$ thick, ranges in color from clear, to faint purple, to dark purple. The cuticle of this membrane, when stained with fast green, appears to be a single layer.

The epidermis throughout the antenna is composed of tall columnar cells that narrow slightly at their bases (Figs. 9, 10). In the proximal segments the cells are taller than the thickness of the cuticle, and in the basal regions

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Fig. 7. Cross section of the pedicel of a one week old adult showing the sensory cells of Johnston's organ (straight arrows). Curved arrows point to branches of the nerve trunk. Mallory's stain. $\times 540$.

Fig. 8. Longitudinal section through the pedicel of a one week old adult showing sensory cells of Johnston's organ. Arrow indicates attachment of the fibers of these cells to the intersegmental membrane between the pedicel and the third segment. Mallory's stain. $\times 1,000$.



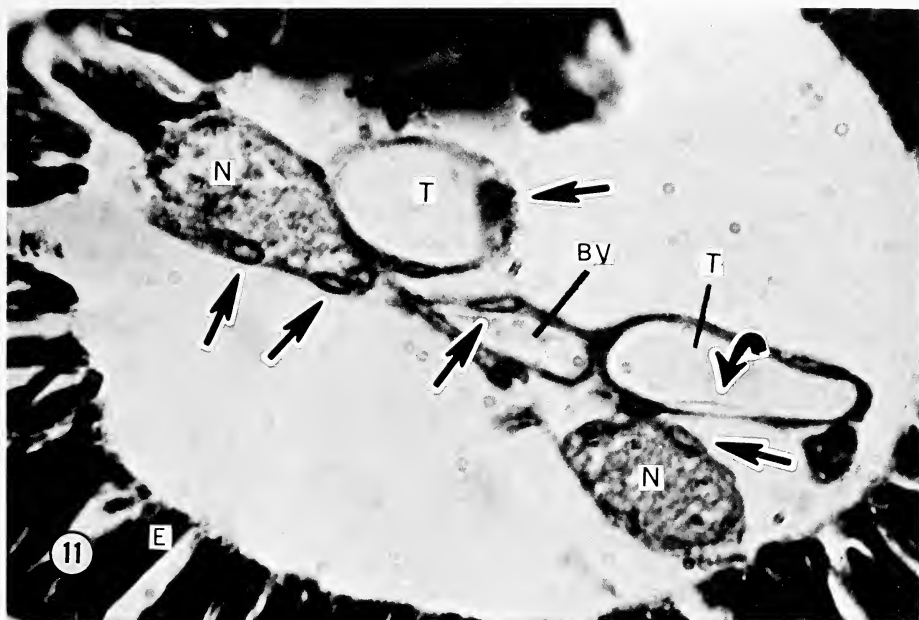


Fig. 11. High power view of a cross section of the antenna of a newly emerged adult showing the arrangement of the nerve trunks, tracheae and blood vessel. Straight arrows indicate nuclei of these various structures and the curved arrow the cuticle of the trachea. Haematoxylin and eosin. $\times 1,000$.

of the distal segments these cells are as tall as the thickness of the cuticle. In the terminal region of the distal segments they are taller than the cuticle. The epidermis is never displaced by nervous tissue even in areas where there are numerous sensory cells. These cells have a large, centrally located nucleus that has both peripheral chromatin and large, round, dense chromatin granules scattered throughout the karyoplasm. The cells stain intensely with safranin and brown yellow to brown red with Mallory's stain. The cytoplasm close to the endocuticle is filled with basophilic granules which also stain faintly blue with Mallory's stain. A very thin basement membrane is visible, which stains faintly blue green with Mallory's stain. The epidermal cells of the intersegmental membrane are very small, cuboidal in shape,

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Fig. 9. High power view of a cross section of the antenna of a newly emerged adult showing the arrangement of the cuticular layers and the epidermis. Haematoxylin and eosin. $\times 1,000$.

Fig. 10. Longitudinal section of the pedicel of a newly emerged adult showing the arrangement of the antennal structures and sensory cells of Johnston's organ. The arrow points to a nerve innervating these sensory cells. Haematoxylin and eosin. $\times 400$.

	<u>ONE WEEK OLD</u>	<u>NEWLY EMERGED</u>
EXOCUTICLE	does not stain	generally does not stain but shows some light red blotches with Mallory's stain
MESOCUTICLE	safranin, eosin, red blotches with Mallory's stain	safranin, eosin
ENDOCUTICLE	haematoxylin, fast green, red with Mallory's stain	haematoxylin, fast green, red with Mallory's stain
INTERSEGMENTAL MEMBRANES	fast green, red and blue with Mallory's stain	fast green, blue and purple with Mallory's stain
EPIDERMIS	safranin, brown yellow and brown red with Mallory's stain	safranin, brown yellow and brown red with Mallory's stain
NERVES	soma: red with safranin and blue with Mallory's stain axons and dendrites: fast green, light blue with Mallory's stain	soma, axons and dendrites: safranin, brown yellow and brown red with Mallory's stain

Table 1. Summary of staining characteristics of antennal structures between one week old and newly emerged adults.

and have a large, centrally located nucleus, similar to the other epidermal nuclei. The basophilic area above the nucleus is also present but it is not as clearly defined as in the cells beneath the endocuticle of a segment. The basement membrane is not discernible beneath these cells.

The central body and axons of the sensory cells resemble the bipolar cells of the one week old adult, except that the dendritic processes are thicker and not as long. In the regions where there are aggregations of sensory receptors the dendrites are very short, while the dendrites for the solitary sense receptors are longer and more closely resemble the dendrites of the older beetle. The cuticle at the apex of the receptor surface of the newly emerged adult is not as sharply defined but appears more blunted than in the one week old adult. The nerve trunk (Fig. 11), the fibers, and the sensory cells all stain readily with safranin and with Mallory's stain, similar to the epidermal cells. At this age there is no way to distinguish nerve cells from epidermal cells other than position and shape.

In the newly emerged adult the nerve trunks and branches are more loose in their arrangement; they are not as compact as are those in the older beetle. However, they are well developed, and many fine nerve branches extend to the sensory cells. Johnston's organ is fully developed in the newly emerged adult (Fig. 10).

The tracheae in this stage are arranged in the same manner as are those in the one week adult. Their walls are thicker, the epithelial cells are taller and the nuclei are larger and not as flat as are those of the older beetle. The tracheal cuticle is clearly visible but its inner surface is not as smooth as that of the older beetle (Fig. 11). The wall of the blood vessel is thicker than that of the one week old beetle, and the nuclei do not bulge into the antennal lumen (Fig. 11). Throughout the antennal lumen, but not within the blood vessel, there is a granular substance which stains with fast green and blue with Mallory's stain.

Discussion

This study shows that the procuticle of the antenna of *Tenebrio* has three layers, and that the mesocuticle is deposited before the endocuticle. The variations of staining characteristics of the different cuticular layers (Table 1) indicates changes in chemical composition. Wigglesworth (1948), Delachambre (1967), and Zlotkin and Levinson (1969) have described only two layers, the exocuticle and endocuticle, in the abdomen of *Tenebrio*. The cuticle of the pupal abdomen was described by Delachambre (1967), Zlotkin and Levinson (1969), and Caveney (1970). Both Delachambre and Caveney mention that the procuticle is composed of two layers, and that the endocuticle is completely deposited within twenty-four hours of pupation.

The epidermis of the antenna undergoes extreme changes during its development. After secretion of the adult cuticle, the epidermal cells are reduced in size and their reduction accompanies the increased development of the nervous tissue. The large, dense, chromatin granules of the epidermal cells of the developing antenna have been seen also in the cells of the abdominal cuticle (Zlotkin and Levinson 1968). The basement membrane is never clearly or completely seen in the antenna of *Tenebrio* because tracheae and nerve fibers adhere closely to the epidermis. The basement membrane is similar to that in the antenna of *Bombyx mori* (Schneider and Kaissling 1959).

Johnston's organ in *Tenebrio* is similar to the one described for the beetle, *Melolontha vulgaris* (Child, 1894). Neither Borden (1968) nor Chang and Jensen (1973) mention this organ in the antennae of the beetles they describe.

Except for the changes in cell thickness, the histology of the tracheae found within the antennal lumen of *Tenebrio* is typical for insects. An antennal blood vessel is described for a coleopteran for the first time and appears similar to antennal blood vessels in other insects. The dilated region of the blood vessel in the third segment may represent an accessory pulsating organ. Schneider and Kaissling (1959) describe a blood vessel in the antenna of *Bombyx mori* that had an opening only at its distal end. The lack of any openings in the blood vessel in *Tenebrio* might be explained on the

basis that small pores may be present in the wall which cannot be resolved by the light microscope. The close association of the blood vessel and the antennal nerve trunk suggests either mutual support or that the blood vessel is innervated.

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(LDT) College of Pharmacy, St. John's University, Jamaica, New York 11439; and (JF) Department of Biological Sciences, Fordham University, Bronx, New York 10458.

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BREEDING EXPERIMENTS WITH *MORPHO PELEIDES INSULARIS*
(LEPIDOPTERA: NYMPHALIDAE) IN TRINIDAD, W.I.

Malcolm Barcant

Abstract.—A breeding program of *Morpho peleides insularis* Fruhstorfer in Trinidad led to successful rearing of large broods of this butterfly on *Paragonia pyramidata* (Bignoniaceae). Crossing with *M. achillaena* Hübn. from Rio de Janeiro, Brazil, gave good fertility to the F₄, while crossing with *Morpho achilles* Fruhst. from Belém, Pará, Brazil did not lead to generations beyond the F₁. The appearance of melanic forms of *peleides*, which occurred on two separate occasions in captivity, was followed by means of selective breeding; this revealed that the melanism had a genetic basis but was probably also influenced by the physical environment (especially excessive sun and heat exposure of juveniles in the breeding cage), and that at least two melanic characters (and possibly three) were segregating independently.

Morpho peleides insularis Fruhstorfer, the only member of its family in Trinidad,¹ is not rare on the island. It is well distributed in all forested areas, particularly along the moist valleys and footpaths of the mountainous Northern Range (Barcant 1970). Very little study has been given to the life history of this species in Trinidad; with the exception of a paper by Stollmeyer (1932), giving details of the early stages obtained from two eggs extruded from the abdomen of a captured female, no further work has been published. Many biological data have recently been published, however, on central American *M. peleides* (Young and Muysshondt 1973; Young and Thomason 1974; Young 1974).

In January 1964, I became interested in breeding Trinidad *M. peleides* in captivity, under near-natural conditions. The following problems had to be solved initially:

a. The butterfly had never been kept alive in captivity in Trinidad; its adaptability to such a life was speculative.

b. The female was a known recluse; only a few existed in collections. It was uncertain whether sufficient numbers in gravid condition could be lured to bait, or whether they would oviposit in captivity.

¹ I have followed Fruhstorfer (in Seitz, 1907) for the nomenclature of *Morpho peleides insularis*. I consider LeMoult's application of the term *tobagoensis* [LeMoult & Real (1962)] to be a misnomer; his recording of subspecies of *M. trojana* and *M. corydon* in Trinidad is also not in accordance with fact.

c. The host plant, *Paragonia pyramidata* Rich. (Bignoniaceae) was known to only two people in Trinidad (it was incorrectly quoted in Stollmeyer's paper), and unknown to me except by vague description—"a forest wild vine with purplish young leaves and not easy to detect."

By mid-1965 these obstacles had been overcome. A fine mesh cage $10' \times 5' \times 8'$ was built; the host plant, located and planted within it, grew rapidly in leafy abundance; and "Emperor Valley" near Port-of-Spain had produced numerous gravid females caught on rotting breadfruit, all willing to lay profusely in captivity. At the end of 1965 two good broods of over 80 adults emerged and the way was open to further study. In February 1966 mating of *M. peleides* in captivity was achieved for the first time in Trinidad; this led to a successful program of breedings and crossings. Further breeding space was also added with another cage of $20' \times 10' \times 8'$.

In early 1966, a visit of Keith Brown, Jr. to Trinidad paved the way for trials in cross-breeding *M. peleides* with *M. achillaena* Hübner from Rio de Janeiro. With his help in the supply of live males from that area, these crossings were performed successfully during 1966. During the year 1967, repeated broods of local *peleides* were raised in one cage and crossing experiments with *achillaena* were continued in the other (until June). Towards the end of the year, the smaller cage was devoted to eventually successful crossings between *M. peleides* and *M. achilles amazonica* Fruhstorfer, from the lower Amazon (Belém). Although the progeny of the latter cross proved sterile, those from the *achillaena* crosses were taken through four generations. In my opinion, this offers strong evidence that *M. peleides* and *M. achillaena* are one species, with morphological differences merely the result of geographical separation, without effect on potential for interbreeding. The relation of both to Amazonian *M. achilles* must still remain an open question, in view of the negative results of the single experiment performed.

Emergence of a melanic form of M. PELEIDES.—In September 1966, during the emergence of the third brood of inbred *peleides*, three males appeared (on 20/IX, 27/IX and 29/IX) with the following characteristics:

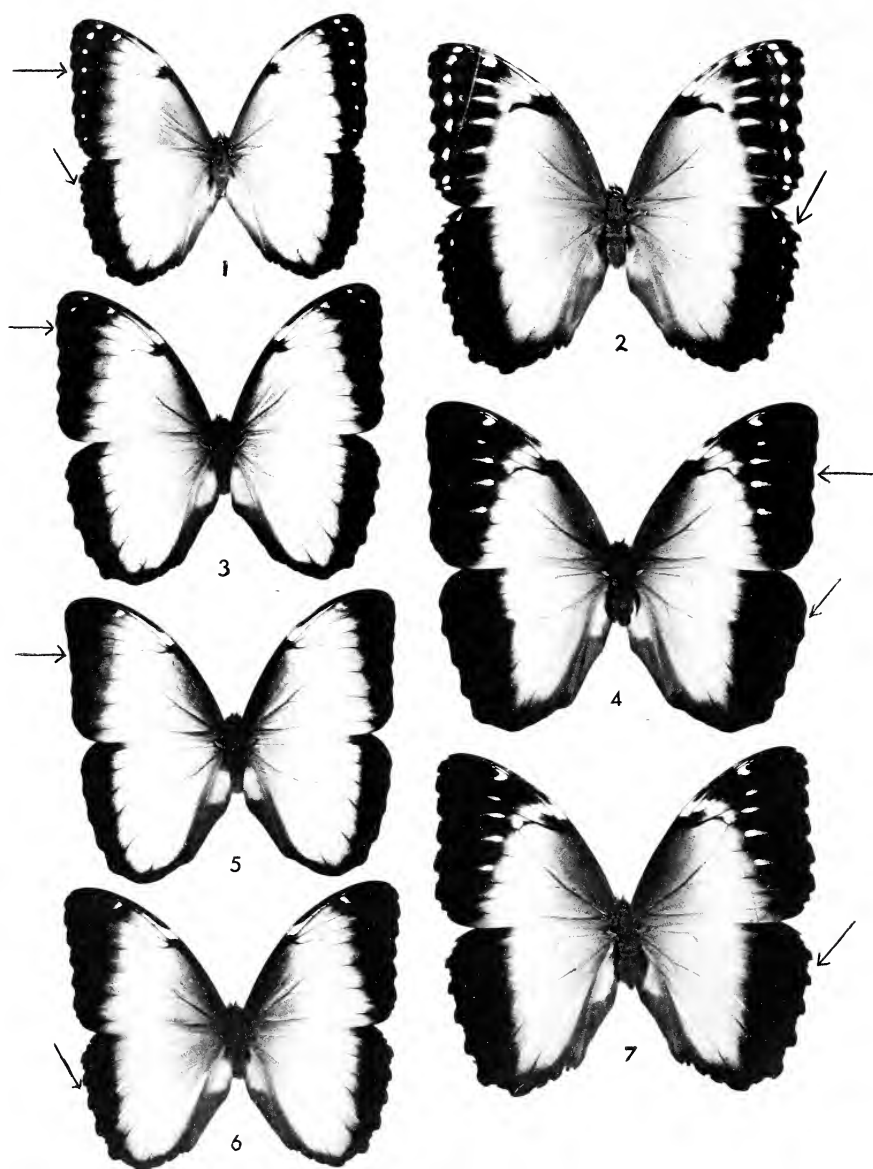
a. Total absence of all white spots in the black forewing submarginal area of the upperside (marginal white spots were still present round the edge of both wings).

b. Total absence of red spottings and cream bands in the submarginal areas of both wings, on the underside.

I expected to get females of this melanic form in the brood, but none emerged, so I was unable to select a melanic pair for inbreeding.

An attempt was made to mate one melanic male with a normal female. This proved unsuccessful, and the event passed by with a notation, the other two melanic males being added to my collection.

No further melanic *peleides* emerged at any time during 1966–1967; it was



All specimens figured were reared in captivity at 19 San Diego Park, Diego Martin, Trinidad, and were selected from Brood 3 described in the text, between November 22, 1968 and January 10, 1969; they are now in the author's collection.

not until early 1968 that melanism again appeared in captive Trinidad *Morpho*.

In March 1968, with the host-plants fully refoliated in the now empty larger cage (after the crossing experiments), five gravid females were captured in the field and set for oviposition, with a full diet of overripe breadfruit (this sweet smelling succulent is abundant in Trinidad, and forms an ideal diet in captivity for all indigenous sugar suckers). Within a week these females had produced 200 eggs, 180 of which hatched. From this successful brood, there emerged 11 melanic males and 10 melanic females during June 2 to 25. The following points were noticeable in these specimens:

a. The males were constant among themselves and identical with the original melanic males produced in September 1966 (Figs. 6, 10).

b. The females, also constant, retained an inner submarginal row of white elliptical spots on the forewing, not as pronounced as in normal females. The outer marginal row was absent. The underside submarginal region of both wings showed the same absence of the three red and cream bands as in the male (Figs. 7, 11).

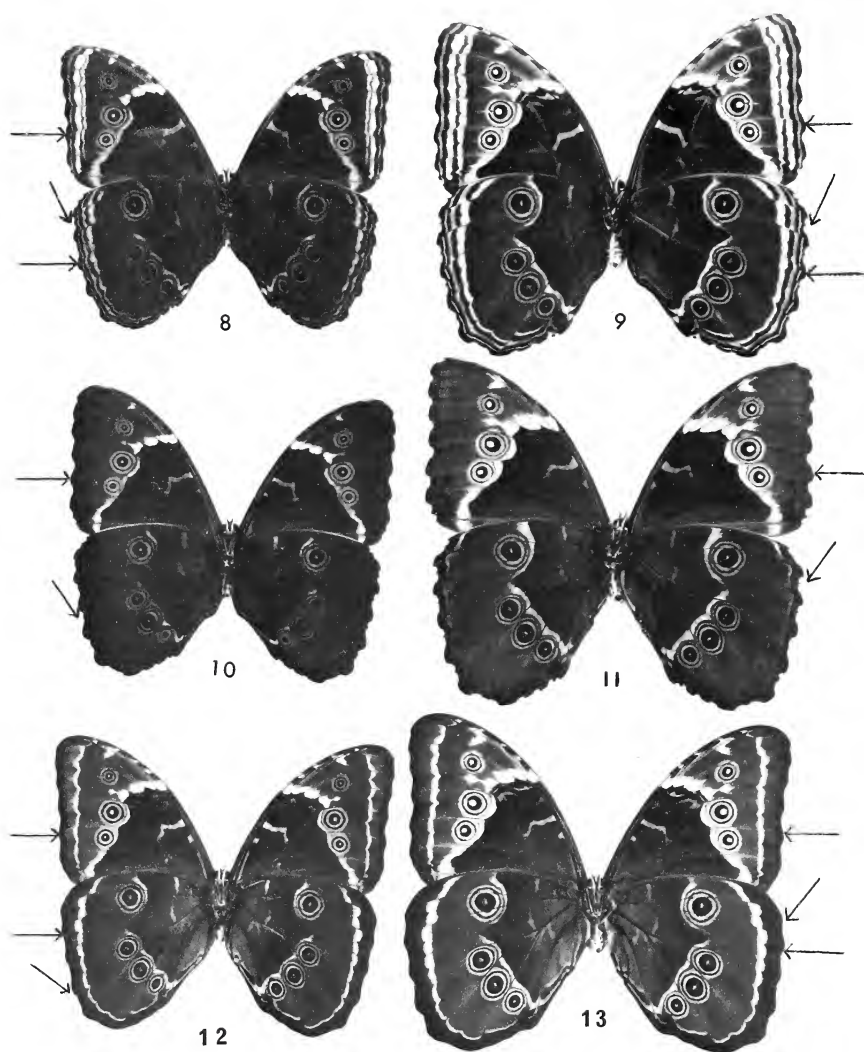
The constancy of the 21 melanic forms suggested the presence of a gene linkage of upperside submarginal white spots and underside submarginal cream and red bands. Selective breeding was carried forward successfully with the melanic individuals from this brood.

Further broods of melanic M. PELEIDES.—On June 9, 1968, four melanic males were put into the cage with four normal females. Matings took place between June 10 and June 14. On June 15, two melanic females were put in with the melanic males. Matings took place within the next two days. Unfortunately, due to space and host-plant limitations, the two groups could not be segregated, and the caterpillars were reared together, leaving a pure black selection for the third brood.

In a total of 83 adults obtained from this "joint venture," 16 (about 20%) were melanic, again constant in phenotype. Due to the mixed nature of this brood little importance can be given to this figure, but it might indicate that

←

Figs. 1-7. (uppersides) Fig. 1. N—Normal male as found in the field; arrows show marginal intervenal white spots on both wings doubled on the hindwing (best noted against the light background by the deeper serrations of the wing margins), and seven submarginal white spots on the forewing. Fig. 2. N—Normal female as found in the field; arrows show marginal intervenal white spots as in the male but more pronounced, and eight submarginal spots on the FW, larger than those of the male. Fig. 3. NRS—"Semi-normal" male, with submarginal FW spots reduced to four (two faint), and intervenal spots present on both wings but not pronounced; the underside is normal. Figs. 4-5. B—Totally black female and male respectively, with both marginal and submarginal spots absent; in the female the inner discal elliptical spots are present but reduced in size. Figs. 6-7. BW—Black male and female respectively, similar to 4-5 except that the intervenal marginal spots are present as in 1-3.



Figs. 8-13. (undersides) Figs. 8-9. N—Normal male and female respectively, with three full submarginal cream and red bands. Figs. 10-11. BW—Black male and female respectively; the three submarginal bands are entirely missing except for a trace at the female HW apex. Figs. 12-13. BC—Totally black (upperside) male and female, respectively; on the underside only the inner of the three submarginal bands remains. Form BCW is similar to 12-13, but with intervenal marginal white spots present.

genetic factors were showing an influence in the appearance of the character. The 16 melanics broke evenly between the sexes and all were used for a third selective brood.

Five matings were obtained between August 31 and September 15, 1968, and egg-laying extended throughout September and the first week of October. No account can be given for the reluctance of three of the females to mate. Surprising deviations appeared in the resulting progeny, which emerged between November 22, 1968 and January 10, 1969. The six phenotypes which appeared in this brood are as follows:

- a. Normal: N (Figures 1, 2, 8 and 9)—normal *peleides*.
NRS (Figure 3)—near-normal *peleides* with forewing submarginal white spots reduced in size and number; otherwise normal with intervenal spots and all underside submarginal bands and red spottings present; this phenotype only in males.
- b. Melanic: BW (Figures 6, 7, 10, and 11)—black form with small intervenal white spots (doubled in female) on the margins.
B (Figures 4 and 5)—totally blackened form, without the intervenal white marginal spots.
BCW (not figured)—black form with white intervenal spots, and one (the inner) instead of three cream bands in the submarginal area of the underside; red spottings absent.
BC (Figures 12 and 13)—same as BCW but intervenal marginal white spots absent.

The following chart indicates the numbers obtained for each phenotype:

Phenotype	Male	Female	Total	
N	30	44	74	} Normal (69%)
NRS	18	—	18	
BW	11	6	17	} Melanic (31%)
B	9	5	14	
BCW	1	2	3	
BC	3	5	8	
Totals	72 (57%)	62 (43%)	134	

The percentage of melanism increased to 31% in this second selective breeding. While the submarginal spots of the forewing upperside and the two outer submarginal bands of the underside were always absent in the

melanic types produced, two types of deviations appeared in the presence or absence of intervenal white marginal spots (W) and the third (inner) cream band on the underside (C). Total disappearance of red from the underside marginal area was observed in all the melanic forms.

The normal cream and red marginal bands expressed themselves as 27% with a single cream band (the inner of the three; BC) and 73% with all three bands completely absent (B). The intervenal white spots divided nearly equally between present (BW, 48%) and absent (B, 52%). The fact that the two characters can be absent together (33%), individually present (W = 41%, C = 19%), or present together (CW = 7%), indicates independence of segregation of the respective genes concerned with cream underside bands and white intervenal spots.

At this stage, it would have been desirable to have unlimited space and host plant available to carry on a growing number of possible combinations. Unfortunately this could not be done, but a fourth brood was obtained on very limited food supply from matings between BW pairs, with the following results:

Phenotype	Male	Female	Total	
B + BW	8	6	14	} Melanic (50%)
BC + BCW	4	1	5	
N	<u>12</u>	<u>7</u>	<u>19</u>	} Normal (50%)
Totals	24 (63%)	14 (37%)	38	

The brood was a small one, and an attempt to score the intervenal spots versus bands was not made, but it may be noted that the single cream band (C) in melanics was again present at 26%.

Due to a change in my residence and the consequent disruption of the breeding experiments, the program had to be discontinued at this stage.

Conclusions and Discussion

I realize that these initial experiments have only scratched the surface of the phenomenon of melanism in Trinidad *M. peleides*; in the absence of more detailed selections and further broods, under controlled environmental conditions, definite conclusions are difficult to make. The evidence from the four broods does indicate, however, that:

- Melanism does occur, potentially, in Trinidad *peleides*, although it has never, to my knowledge, been recorded in the field; it was discovered for the first time in breeding experiments in September 1966.
- Genetic factors play a predominant role in the expression of melanism in Trinidad *peleides*: it seems probable that a 100% pure melanic strain could be developed by repeated selective breeding.

- c. Selective breeding does bring out more than one expression of melanism, with varying combinations of the presence or absence of the three normal pattern features.
- d. Morphologically, in habits and in lifespan, the early stages of the melanic *peleides* are identical to those of the normal form.

In the absence of more detailed experiments, the initial cause for the development of melanism in the captive populations can only be speculative. In the face of a 10% development in the first brood, from normal parents obtained directly in the field, where the phenomenon has not been recorded, it is necessary to consider that the color modification may be due to environmental stress under captive conditions.

In all the broods, it was observed that the host plant climbing against the mesh roof of the cage was mostly sparse in growth, not only letting through sunlight but in many areas having only a single thin layer of older leaves exposed to the direct rays of the sun. Caterpillars which in the field would invariably be well shaded by thick overhead forest growth throughout their five instars, therefore found themselves exposed to a much higher degree of direct sunlight than they would normally experience. In many cases, they found large leaves at lower levels on the sides of the cage, where they could be sheltered under more normal conditions of temperature and shade, but some persisted at higher levels near the roof of the cage. In the heat of the day, these could be seen hanging downwards by their hind pair of fleshy prolegs, possibly in response to heat stress or to escape the high temperature and sun's rays which were penetrating and heating the leaves below which they had been resting.

It is possible that the existence of such abnormal conditions of heat and light during the first four instars, perhaps to a lesser degree in the fifth when the caterpillars became gregarious and hid along the stems of the vine, but also in the pupal stage when they were often on the cage roof again (though in seclusion), could affect the expression of some genes controlling the marginal spots and underside bands, and that this effect could be continued increasingly by selective breeding in successive generations.

The proportional numerical increase in melanic emergence through selective breeding suggests that recessives, normally obscure in the field, were concentrated in the later broods, though their expression may also have been triggered by abnormal environmental conditions. It is difficult, however, to propose a mechanism whereby additional heat, sunlight and exposure could promote melanism in the adults.

Acknowledgments

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731 West Daughtery Road, Lakeland, Florida 33805.

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PARASITISM OF SINGLE AND MULTIPLE EGG CLUSTERS OF
EUPHYDRYAS PHAETON (NYMPHALIDAE)

Nancy E. Stamp¹

Abstract.—The effect of egg numbers on parasitism of *Euphydryas phaeton* (Nymphalidae) was examined by comparing single and multiple egg clusters on leaves. Some 65 to 80% of the clusters lost eggs to parasitism and predation, with 5 to 9% of the eggs lost per cluster. For total clusters, single clusters and multiple clusters, the numbers of parasitized clusters were significantly different between years. It appeared that when the overall level of parasitism was greater one year, multiple clusters were attacked more frequently than single clusters. However, the number of egg clusters per leaf had no effect on the number of parasitized eggs per cluster. The sequence of egg clusters deposited on a leaf did not affect the level of parasitism and number of parasitized eggs per cluster. Thus, these egg clusters composed of several hundred eggs each lost only a small fraction of eggs to parasitoids and predators and did not appear to benefit from aggregation of egg clusters.

Introduction

The patterns of egg distribution by insects are varied; with some insects depositing eggs singly, others depositing many small clusters of eggs, and others laying a few large clusters. Eggs deposited in clusters may have higher survivorship than those laid singly (Stamp 1980a). Furthermore, parasitoids may differ in their efficiency at exploiting various sizes of egg clusters (Hokyo and Kiritani 1966). Egg parasitoids specializing on a host depositing eggs singly, attacked fewer eggs when those eggs were clustered, as a consequence of reduced encounters with total host eggs and limited mature eggs for oviposition (Hirose et al. 1976). In contrast, for parasitoids adapted to eggs occurring in clusters, large clusters were found more frequently and had higher parasitism than small clusters (Lyons 1962). This may be a consequence of the searching behavior of animals which concentrate their efforts in areas where they recently found prey (Laing 1937, Tinbergen et al. 1967, Royama 1970). Also, as immobile host patches, large clusters may be advantageous to parasitoids and predators as the overall distances between clusters increases (e.g. Janzen 1975). Thus, egg parasitoids searching for large egg clusters may deposit all or most of their eggs in one or a few places

¹ Department of Zoology, University of Florida, Gainesville, Florida 32611.

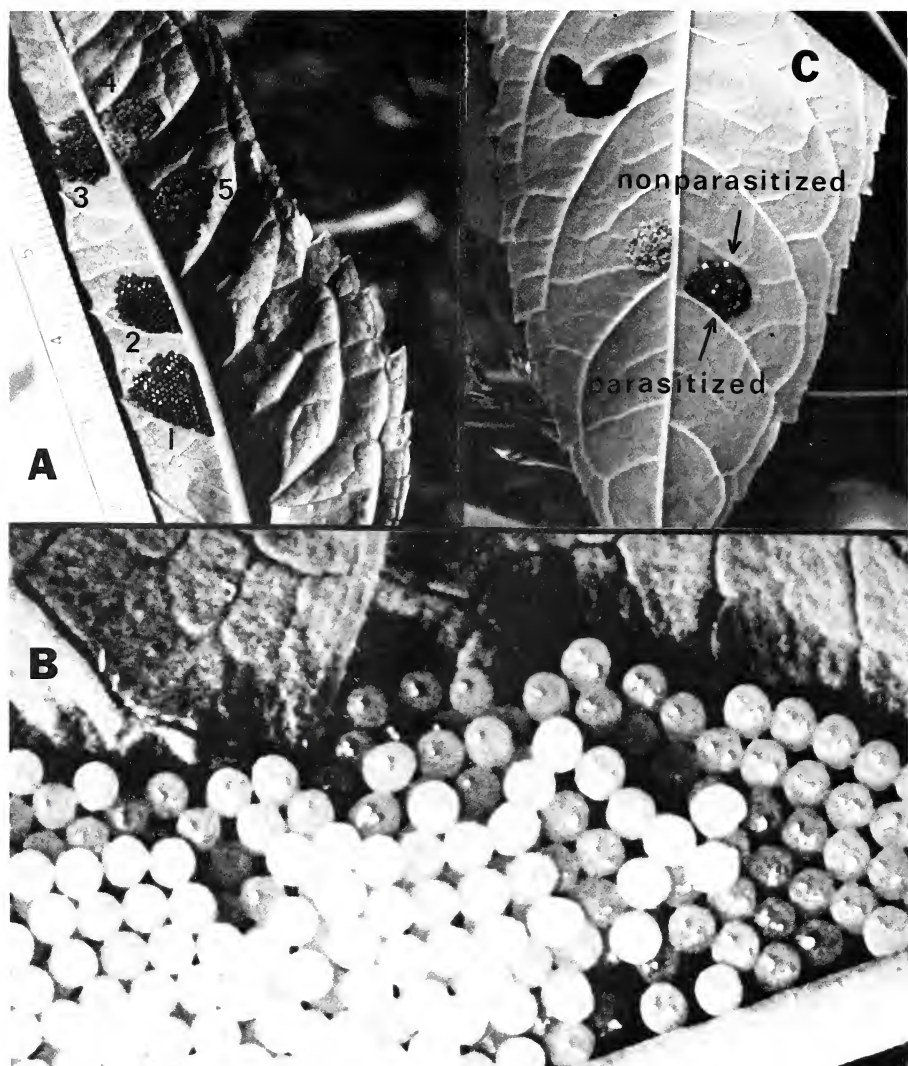


Fig. 1. Egg clusters of *E. phaeton*. A. Five clusters deposited on the same leaf by five females. Scale is in cm. B. Eggs are laid in layers. C. The egg cluster on the right is 9 or more days old and has some parasitized (black) eggs. The egg cluster on the left is 4 days old.

and, thus, benefit by spending less time searching and exposing themselves to mortality factors.

Whether the hosts or parasitoids benefit more from clustered eggs may be examined in differing but naturally-occurring group sizes of eggs. The Baltimore checkerspot (*Euphydryas phaeton* Drury: Nymphalidae) is suitable for this study because it deposits large egg clusters ($274 \text{ eggs} \pm 23 \text{ SD}$

per cluster, Stamp 1980b). Frequently females lay eggs with those of other females (Fig. 1A). Of 483 leaves with egg clusters, 18% had multiple (two or more) egg clusters (Stamp 1980b). The eggs are parasitized by an undescribed trichogrammatid wasp (David Vincent and Carll Goodpasture, unpublished). Thus, the advantages of clustering eggs can be evaluated by examining parasitism of single and multiple egg clusters on leaves. For comparison, numbers of missing eggs as an indicator of egg predation were determined also.

Materials and Methods

A population of *E. phaeton* was observed at the Conservation and Research Center of the National Zoological Park at Front Royal, Virginia in 1978 and 1979. Turtlehead (*Chelone glabra* L.: Scrophulariaceae) the larval host plant grew in wet meadows along one drainage. In each year about 500 egg clusters were deposited in this study area. Egg clusters consisted of eggs deposited usually in two layers, with a typical nymphalid egg shell and moderate adhesion to the leaf (Fig. 1B).

New egg clusters on tagged plants were photographed with Kodachrome film. The bright yellow coloration of new clusters differentiated them from older (5 to 24 days), tan to red egg clusters. Females sometimes deposited eggs adjacent to those of another female. The newer egg clusters were easily distinguished from the older clusters by coloration. The egg clusters were rephotographed 15 to 20 days later. At that time the black, parasitized eggs were readily distinguishable from the red, unparasitized eggs (Fig. 1C). From the photographs I counted the eggs to determine the original numbers deposited. Due to layering of eggs in the clusters, the margin of error for egg counts was 5.5% of the mean eggs per cluster. This was determined by photographing 32 clusters, estimating the number of eggs per cluster from the photograph, and then counting the number of eggs per cluster using a dissecting microscope.

The number of missing eggs was calculated by counting eggs in the rephotographed clusters and comparing that to the original numbers deposited. Empty egg shells and partial egg shells were classified as missing eggs. Although some of the missing eggs may have been lost due to abiotic factors (e.g. Dempster 1971, Root and Chaplin 1976), most were probably lost to predators (e.g. indirect evidence from Ives 1967; Owen 1971; Ehrlich and Gilbert 1973; Gilbert 1975; Rausher 1979a, 1979b; Stamp, pers. observ.). Thus, I considered missing eggs as representative of those eaten by predators.

To determine egg parasitism, the black eggs in the rephotographed clusters were counted. These numbers were not affected by layering of eggs because the parasitized eggs were only found in the exposed layers of the

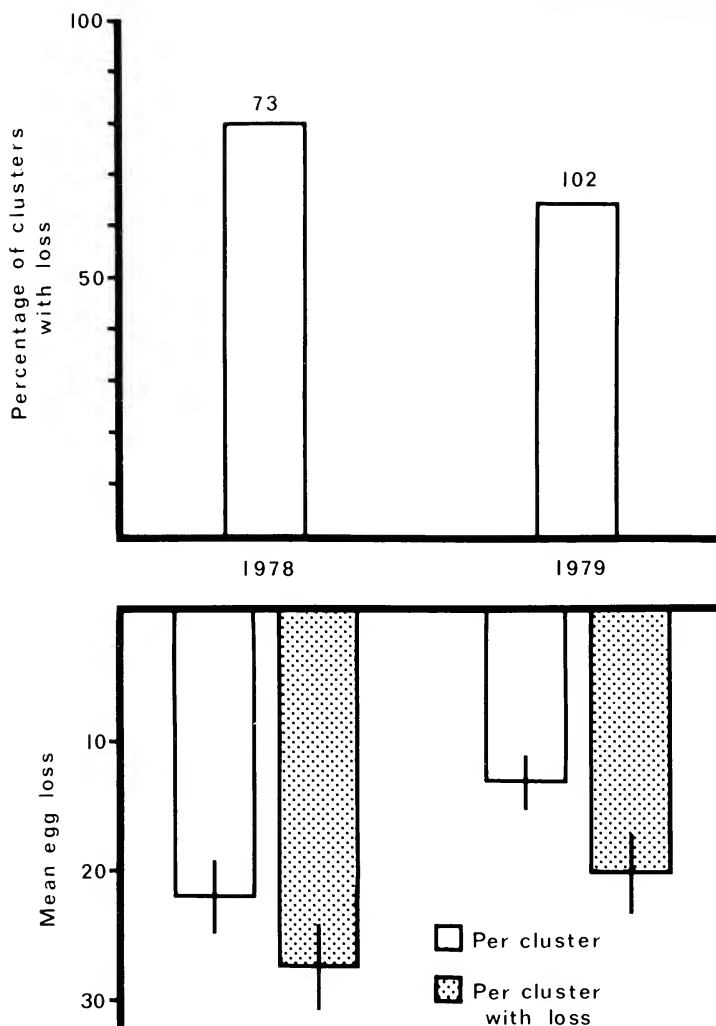


Fig. 2. Total egg loss between years. Numbers above bars are total egg clusters, and \pm one standard error is indicated for mean egg loss. The proportion of clusters with egg losses (missing and parasitized) differed significantly (χ^2 -test, $P < .05$). Mean egg loss for all clusters and mean egg loss for only those clusters with losses were both significantly different between years (all clusters, two-sample t test, $P < .001$; clusters with loss, two-sample t test, $P < .05$).

clusters. In addition, egg clusters rephotographed in late June 1979 ($n = 102$) and clusters collected two weeks later in July ($n = 120$) were examined for parasitism. For 29 leaves the sequence of clusters deposited was determined based on egg coloration. Fifteen of these leaves had one or more parasitized cluster, for a total of 19 parasitized clusters. Parasitism rates for the first cluster and clusters deposited later were compared.

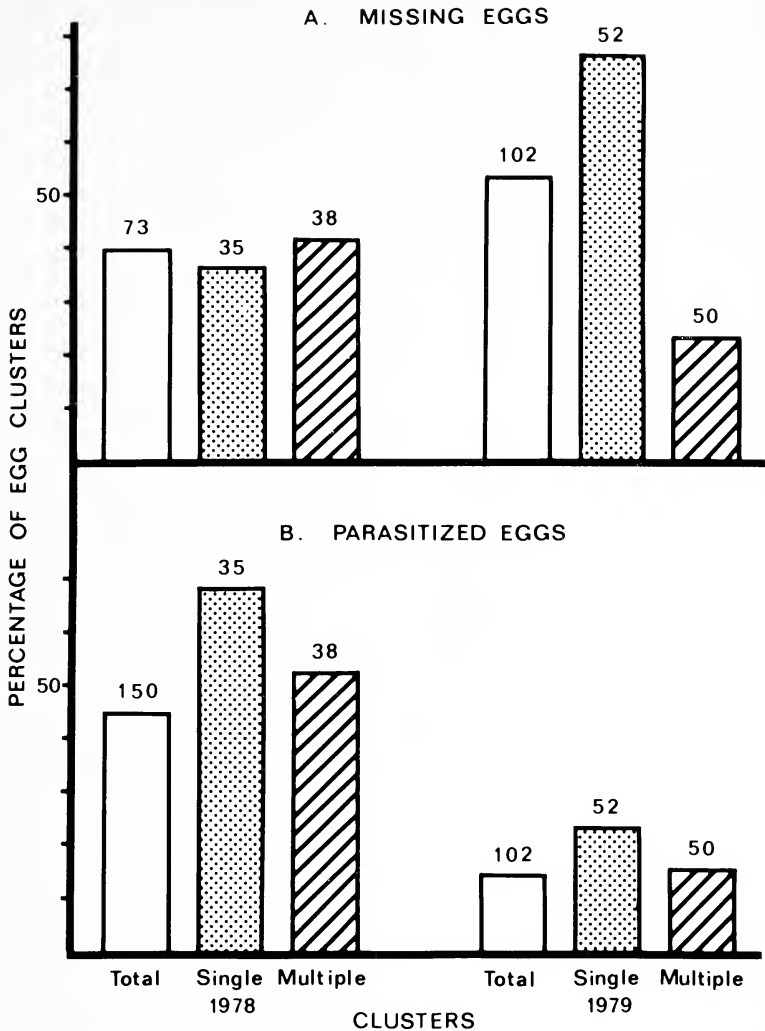


Fig. 3. Percentages of egg clusters with missing eggs and parasitized eggs. Percentages are given for total clusters, single clusters, and multiple clusters. Numbers of clusters are indicated above bars. Of the 150 clusters in 1978, 73 were classified as single or multiple clusters. A. Missing eggs: for single clusters between years, χ^2 -test, $P < .025$; for single and multiple clusters in 1979, χ^2 -test, $P < .001$. B. Parasitized eggs: for single clusters between years and for multiple clusters between years, χ^2 -tests, $P < .001$ and $P < .005$, respectively. No significant differences occurred between single and multiple clusters within years (χ^2 -tests, $P > .25$).

Results

Total clusters.—Some 65 to 80% of the clusters lost eggs (parasitism and predation), and from 5 to 9% of the eggs per cluster were lost ($n = 73$ and 102 clusters for 1978 and 1979, respectively; Fig. 2). Most clusters with egg

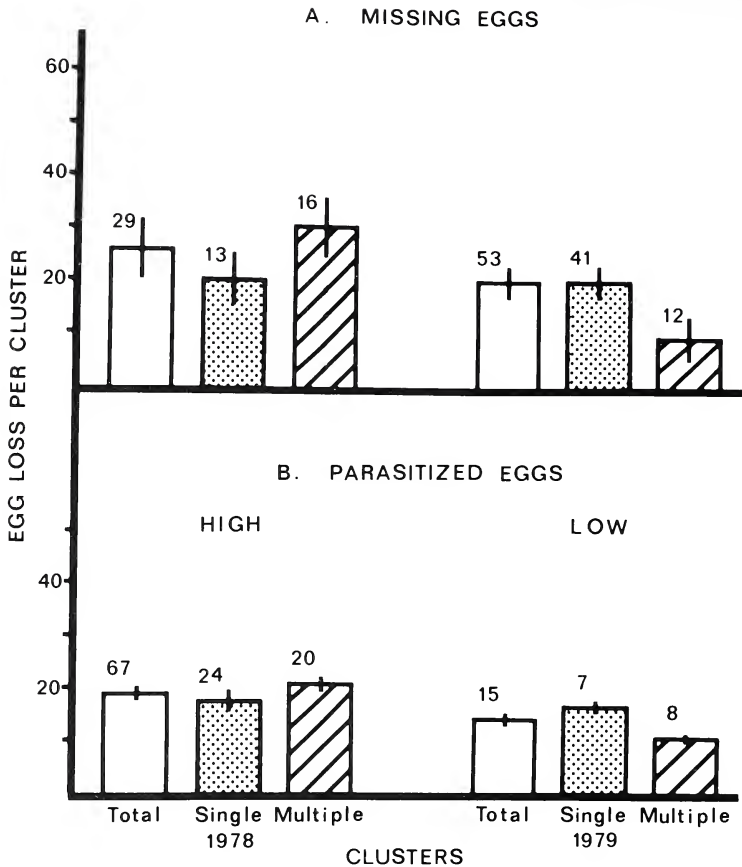


Fig. 4. Mean numbers of missing and parasitized eggs per cluster with egg loss. Means are given for total clusters, single clusters, and multiple clusters, with \pm one standard error. Numbers of clusters with egg loss are indicated above bars. Of 67 parasitized clusters in 1978, 54 were classified as single or multiple clusters. High and low refer to a relatively high or low overall rate of parasitism between years as indicated in Fig. 2B. A. Missing eggs: for single and multiple clusters in 1979, and for multiple clusters between years, Mann-Whitney U test, $P < .05$. B. Parasitized eggs: for single and multiple clusters in 1978, Mann-Whitney U test, $P < .001$; but for single and multiple clusters in 1979, Mann-Whitney U test was not significant ($P > .05$).

loss lost a few eggs (less than 20), but a few lost as many as 40 or more. The proportion of total clusters with missing eggs were similar between years, as were the mean losses per cluster (Figs. 3A and 4A). Some 4% of the eggs per cluster were missing. Chrysopid larvae, coccinellid larvae and pentatomid nymphs were observed at egg clusters. In contrast to missing eggs, the numbers of total clusters with parasitized eggs and the mean losses per cluster were significantly different between years (Figs. 3B and 4B). Generally, less than 5% of the total eggs were parasitized. During the egg

deposition period (June), clusters laid later in the month had a level of parasitism similar to those laid earlier in June (χ^2 -test, $P > .10$), but mean loss per cluster was higher in July than in June (normal approximation to Mann-Whitney U test, $n_1 = 28$ and $n_2 = 102$, $P < .001$). Thus, egg clusters attacked by predators and parasitoids and which were composed of several hundred eggs lost only about a tenth of the eggs (e.g. 27 eggs lost ± 26 SD in 1978).

Single and multiple clusters.—The proportion of egg clusters attacked by predators varied considerably between years for single clusters and between single and multiple clusters in 1979 (Fig. 3A). Egg losses due to predation also varied from year to year, with less on multiple clusters than on single clusters in 1979 (Fig. 4A).

The numbers of parasitized clusters were significantly different between years for single clusters and for multiple clusters (Fig. 3B). However, the number of egg clusters per leaf (that is, single compared to multiple clusters) had no disproportionate effect on the number of parasitized eggs per cluster (Mann-Whitney U test for 1978 and 1979 combined; $n_1 = 20$ and $n_2 = 22$ for single and multiple clusters, respectively; $P > .05$). The sequence of egg clusters deposited did not affect the level of parasitism and number of eggs parasitized (for clusters attacked, χ^2 -test, $P > .10$; for parasitized eggs, Mann-Whitney U test, $P > .10$).

Discussion

The number of parasitized eggs among *E. phaeton* clusters was probably a function mainly of three factors. 1) The distribution of *E. phaeton* clusters in these wet meadows was clumped (Stamp 1980b) and most likely was clumped relative to the parasitoids' habitat (e.g. Flanders 1937). Consequently, some egg clusters escaped parasitism and predation. More parasitized eggs in multiple clusters than in single clusters when overall egg parasitism was high suggests that these egg parasitoids may cue on the large, clumped resources of clusters. Cheke (1974) found that the area of discovery was higher for randomly dispersed egg clusters when parasitoid (*Alaptus fuscus* Haliday: Mymaridae) densities were low whereas when parasitoid densities were high, multiple clusters were attacked more efficiently. 2) The variation in numbers of eggs attacked (range 1 to 93 parasitized eggs per cluster) indicates that some clusters were used by two or more parasitoid females. 3) The age of the eggs when located by parasitoids may determine host acceptance (Lewis and Redlinger 1969, Vinson 1976). Furthermore, the change in egg coloration (yellow to red) followed by the pale green coloration of the newly-hatched larvae suggests that these eggs may contain toxins (e.g. Stamp 1980a) and, thus, such toxins may restrict the period when eggs are acceptable to parasitoids and predators.

The variation in clusters attacked by predators and loss of eggs was prob-

ably a result of the clumped distribution of egg clusters in the habitat, mobility of the egg predators (mainly nymphs and larvae rather than winged insects), and wide variety of generalist predators using these eggs. For example, the greater loss of eggs from single clusters compared to multiple clusters in 1979 but similar losses between single and multiple clusters in 1978 appeared to be a consequence of the random distribution of the set of egg predators in this habitat. Ives (1967) suggested that overall egg mortality of the larch sawfly *Pristiphora erichsonii* (Hartig) was unrelated to predator density due to the random distribution of the predators in contrast to the clumped distribution of eggs, but that once egg predators located clusters they remained near the eggs and fed periodically. The clumped distribution of missing eggs within clusters of *E. phaeton* supports this.

Finally, for *E. phaeton* females, depositing eggs with those of other females appeared to have no effect on levels of egg parasitism and predation. Perhaps later-deposited clusters benefited from nearby predators satiating themselves on the first cluster, but in one case the second cluster deposited of three on a leaf was almost completely destroyed by a predator whereas the other two clusters lost only a few eggs each. Similarly, later-deposited clusters had the same level of parasitism as the first clusters deposited per leaf. Consequently, the advantage of depositing clusters with those of other females was unrelated to the sequence of cluster deposition on a leaf. Thus, in this host-parasitoid system, egg clusters composed of several hundred eggs lost a small fraction of eggs to parasitoids and did not benefit from aggregation of egg clusters.

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Department of Zoology, University of Maryland, College Park, Maryland 20742.

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SOME OBSERVATIONS ON SOARING FLIGHT IN THE
MOURNING CLOAK BUTTERFLY (*NYMPHALIS*
ANTIOPA L.) IN SOUTHERN ONTARIO

David L. Gibo

Abstract.—The Mourning Cloak butterfly, *Nymphalis antiopa* L., is capable of soaring flight. The adults appear to recognise rising air currents and exhibit complex behaviour patterns to stay inside these systems. The soaring behaviour of *N. antiopa* is similar to that of monarch butterflies, *Danaus plexippus* L.

Soaring flight consists of maintaining or gaining altitude by gliding in rising air currents (Conway 1969; Gibo and Pallett 1979). Consequently, a soaring animal is actually remaining aloft by extracting energy from the atmosphere. Although soaring flight is the most efficient form of flight possible in terms of energy expenditure per unit of distance travelled (Pennycuick 1969), deliberate use of this flight technique has only been reported for two insects, the monarch butterfly, *Danaus plexippus* L. (Gibo 1981; Gibo and Pallett 1979; Schmidt-Koenig 1979), and the dragonfly *Pantala flavescens* Fabricius (Hankin 1921). The apparent rarity of this flight technique among insects may be due to the need for complex behaviour patterns (Gibo and Pallett 1979; Hankin 1921; Pennycuick 1969, 1972, 1975), special sensory systems (Johnson 1969), and specific meteorological conditions (OSTIV 1978). During a 9 day period in the late summer of 1979, while observing the flight of migrating monarch butterflies, *Danaus plexippus* L., in southern Ontario, I was also able to observe the flight techniques of mourning cloak butterflies, *Nymphalis antiopa* L. Three of the 11 *N. antiopa* observed were soaring. This note is a preliminary report on the soaring behaviour of *N. antiopa*.

One observation was made in an open area on the Erindale College Campus of the University of Toronto and two were made in an open area 3 km to the west of the campus. The times ranged from noon to midafternoon. Wind velocities at 1 m above the ground were measured with a wind meter. The courses of the butterflies were determined with a compass. The air temperature at 1 m was also measured. The estimated altitude of the butterfly above the ground was recorded and any significant manoeuvres performed by the soaring butterflies, such as circling, were noted.

Two of the soaring *N. antiopa* were observed to enter thermals (rising bubbles or columns of relatively warm air produced by convection). The first individual, observed on 4 September at 12:03 P.M. (E.S.T.), flew overhead at an altitude of 20 m. The wind direction was 165° and the velocity

was 5 km/hr. Initially the butterfly employed powered flight and maintained a 225° (SW) course. Suddenly, presumably upon encountering a thermal, the butterfly stopped beating its wings and began soaring in circles 1 m in diameter. After gaining approximately 10 m in altitude and simultaneously drifting approximately 50 m downwind on a 325° (NW by W) track, the butterfly abruptly resumed powered flight and reestablished its former SW course.

The second individual, observed on 5 September, gave an impressive demonstration of its ability to locate and exploit a weak thermal. When the butterfly was first observed (11:45 P.M., E.S.T.), it was flying under power at a height of 1 m and was maintaining a SW course. There was no apparent wind within 2 m of the ground. As the *N. antiopa* passed over a paved parking area 5 m from the observation point it suddenly began to climb, still beating its wings, until it reached a height of 3 m. It then stopped beating its wings and began soaring in circles. The butterfly did not beat its wings again for the rest of the observation: a period of 2 minutes. Initially the butterfly flew in circles approximately 3 m in diameter remaining directly over the parking area. It gained altitude gradually and required about 1.5 m to reach a height of 15 m. Apparently there was a light northeast breeze at this height because the butterfly then began to drift on a 215° (SW by S) course, reducing the size of its circles to approximately 1 m in diameter. For the remainder of the observation the butterfly continued to soar in 1 m circles and drift on a 215° (SW by S) track. When the *N. antiopa* reached an approximate altitude of 25 m and a distance of 80 m, I could no longer determine whether it was still gliding (i.e. not beating its wings) and terminated the observation.

The third individual was observed on 8 September. The *N. antiopa* was already soaring overhead in a thermal when first noticed. The time was 2:38 P.M. (E.S.T.). The wind direction was 105°, and the velocity was 5 km/hr. This butterfly was at an altitude of 20 m and soared in circles of approximately 1 m in diameter while drifting overhead on a 285° (W by N) course. This last specimen neither gained nor lost altitude, but simply drifted downwind until it was lost from sight.

The mourning cloak has long been known to migrate in Europe (Williams 1942, 1958) and there is evidence that at least part of the population in eastern North America migrates (Shannon 1917). Frequent episodes of soaring would significantly reduce the energy expenditure of this activity. It is interesting to note that the mean course and angular deviation (see Batschelet 1965) of the 11 *N. antiopa* in this study was $246^\circ \pm 30.3$ (WSW), which is similar to the SW to SSW courses frequently reported for migrating *D. plexippus* (Beall 1941; Schmidt-Koenig 1979; Urquhart 1960; Urquhart and Urquhart 1978).

The mourning cloak butterfly is the second butterfly found to exhibit

specialized soaring behaviour. The soaring behaviour observed for *N. antiopa* in thermals was similar to the behaviour reported by Gibo and Pallett (1979) for *D. plexippus*. Individuals of both species are apparently able to detect and enter thermals both near the ground and well above the ground. In addition, adults of both species are able to remain within thermals by soaring in circles. The presence of this highly specialized behaviour in members of two distinct families of butterflies (Danaiidae and Nymphalidae) suggests that the ability to soar may be widespread among butterflies.

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Department of Zoology, Erindale College, University of Toronto, Mississauga, Ontario L5L 1C6, Canada.

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OBSERVATIONS ON THE SPRING AND SUMMER BEHAVIOR OF
THE 12-SPOTTED LADYBIRD BEETLE, *COLEOMEGILLA*
MACULATA (DEGEER) (COLEOPTERA: COCCINELLIDAE)

Allen H. Benton and Andrew J. Crump

Abstract.—The twelve-spotted ladybird beetle, *Coleomegilla maculata* (DeGeer) was studied at sites in western and central New York from 1973 to 1980. Aggregations of overwintering beetles begin to be active in April, and dispersal occurs gradually from then until late May. During this time, beetles feed on pollen of a variety of flowers in and near the aggregation site. After dispersal and a period of feeding, mating occurred near the end of May. Summer generations moved into cornfields when the corn was large enough to provide pollen and/or aphids. Sweet corn in this area may reach this size by early July, field corn by early August. The daily activity cycle of the beetles appeared to be based on geotaxis, with upward movement occurring in the early daylight hours and downward movement occurring in late morning. A positive hygrotaxis may also be involved in the downward movement, as the higher locations begin to become drier as the day advances.

During dispersal, beetles showed a strong preference for yellow in color preference tests in the laboratory, and were commonly found on yellow flowers in the field. Once dispersed, this preference disappears and no clear pattern of color preference is shown. This phenomenon may have some bearing on the fact that dispersing beetles tend to fly in the direction of the sun.

Introduction

The twelve-spotted ladybird beetle, *Coleomegilla maculata* (DeGeer), is a common Coccinellid throughout temperate North America and northern Europe. The species has been well studied, beginning with the pioneering study by Riley (1893). More recent studies include those of Hodek (1967) in Europe, Balduf (1935), Hagen (1962), Ewert and Chiang (1966) and Smith (1971). In a previous paper from this laboratory (Benton and Crump, 1979) we have discussed overwintering aggregations in this species. The present paper discusses the behavior of this beetle from the time of spring dispersal until the formation of the overwintering aggregation.

Methods and Materials

Winter aggregations of *C. maculata* were observed in the town of Pomfret, Chautauqua County, New York, and in the town of Victory, Cayuga

County, New York. Most of the observations on dispersal were made at the Cayuga County site. Post-dispersal observations were made at both locations, while summer generations were studied near the Chautauqua county site. Several hundred beetles were used in a series of laboratory experiments related to sensory perception, including reaction to light, temperature, relative humidity, color and odors. Dispersal patterns were observed in the laboratory by releasing beetles in a greenhouse at the appropriate time.

Spring Dispersal

While the process of aggregation in the autumn occurs within a week or two (Benton and Crump, 1979), dispersal is a much more prolonged process. The beetles become active after a few days of warm weather, even if they occur during the winter months. Usually the first few warm days in early- to mid-April cause the beetles to move up grass stems or other plants in preparation for dispersal from the overwintering site. If pollen is available at or near the aggregation area, they will begin to feed. In early May, many beetles were found on male catkins which had fallen from the cottonwood (*Populus deltoides*) at the base of which an aggregation had formed and shortly thereafter on dandelions up to ten meters from the aggregation site. At other locations, we have found large numbers (up to 10 per flower) on the cowslip (*Caltha palustris*), and smaller numbers on a variety of other spring flowers. No preference for specific flowers was noted, although the greatest numbers have been found on bright yellow flowers such as cowslips and dandelions. However, these are often the most abundant large flowers in the vicinity of aggregations, so they are obvious choices for efficient pollen feeding. The preference of dispersing beetles for yellow, as noted below, may or may not be related to the presence of yellow flowers during the gradual dissolution of the aggregation.

On May 4, 1980, beetles were counted on dandelion flowers within 10 meters of the Cayuga County aggregation. Feeding began shortly after sunrise, with the first beetle observed on a flower at 5:30 a.m./EST. From then until 9:30, the numbers increased steadily, reaching a peak of 32 individuals at 9:30/EST. By 10:00 a.m., the number had dropped to 19 and counting was discontinued. This agrees well with summer observations noted below (see Fig. 1).

Fanwise dispersal from the aggregation has been reported for this species (Allee, 1949). A possible mechanism for attainment of this sort of dispersal might be flight in the direction of the sun. As the day advanced, beetles would fly successively in a more westerly direction, and would thus be dispersed over a wide area. To investigate this, we placed a group of 50 beetles in a darkened box at the time when the aggregation was dispersing. The box was opened in a greenhouse, and the beetles crawled to the top of the box and took off in the direction of the sun. For several hours, the beetles re-

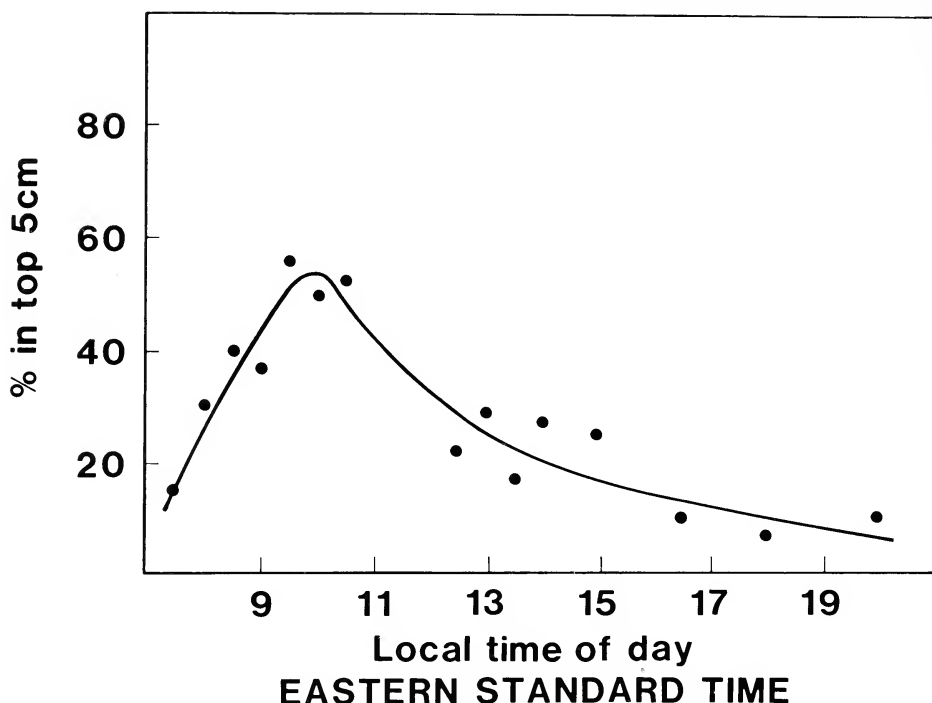


Fig. 1. Vertical distribution of adult *Coleomegilla maculata* during daylight hours under laboratory conditions. See text for details.

maintained clustered at the top of the greenhouse in a direct line from the box toward the sun.

As noted above, beetles emerging from the aggregation occurred most commonly on yellow flowers. Coupled with the direct sunward flight on dispersal, this suggested an attraction for bright yellow at this time. We tested this in the laboratory by placing colored cards of equal size in an area 30 cm square and 10 cm high. The reflectivity of the cards was not measured. Groups of beetles were placed in the arena, which was lighted from above by fluorescent lights, and their locations checked at intervals. At the time of dispersal, 90% of the beetles remained on yellow and white cards after one hour, indicating initial preference for light colors. When similar tests were conducted with free-ranging beetles collected in June and August, no clear color preference was evident.

Mating may occur before the beetles leave the aggregation, though long term observations have not revealed it. It is more probable that a period of breeding is necessary before mating. Adult beetles collected from flowers in Chautauqua County on May 15, 1979, were placed in a large jar as they were collected. By the time they were transferred to the laboratory, most of them were mating. We maintained these beetles in the laboratory under natural

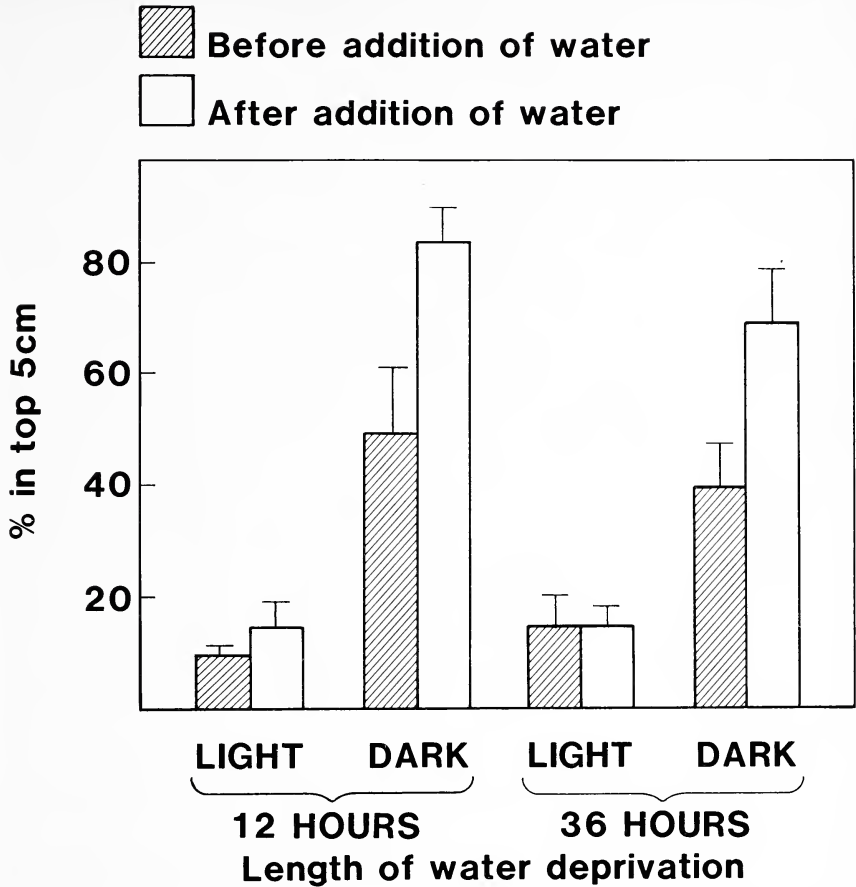


Fig. 2. Vertical distribution of adult *Coleomegilla maculata* after water deprivation, before and after addition of water to the substrate. See text for details.

conditions of light and temperature, but no oviposition was observed and all beetles died within 30 days.

Although *C. maculata* may be found in small numbers in a variety of habitats in summer, most individuals tend to congregate in corn fields, making them readily available for study. By early July, local fields of corn (*Zea mays*) have reached a size adequate to supply aphids, while sweet corn fields may supply abundant pollen by mid-July. Both adult and larval beetles may be found on the corn in great numbers, feeding on both aphids and pollen of the corn, for the rest of the summer, leaving the corn only to move to the aggregation site.

Adult beetles were found on exposed leaves and stems only during the morning hours (7–11 EST). At other times, they could be found in rolled-up

leaves, leaf axils or on the ground around the bases of the corn plants. Field observations showed that beetles climbed or flew to the upper levels of the corn in the early morning hours, and descended to lower levels or to leaf axils before noon. Several possible reasons could explain this vertical movement: 1) Positive phototaxis might cause upward movement as the sun rose. This appeared unlikely, since downward movement was completed while the sun was still moving toward its zenith. 2) Rising temperature might stimulate feeding activity. This, too, seemed unlikely, since the downward movement occurred while the temperature was still rising. 3) Negative geotaxis might initiate upward movement at sunrise. Observations in both field and laboratory showed that beetles tended to move upward on any vertical object available to them, suggesting a geotactic response. The most obvious explanation for the downward movement was a positive hygrotaxis of sufficient strength to overcome the climbing tendency. Obviously, a reversal of the geotaxis or a negative phototaxis would have the same result.

This phenomenon was investigated in the laboratory. Ten groups of ten beetles each were placed in 10 cm \times 24 cm glass bell jars with netting over them. The jars were about $\frac{1}{4}$ filled with moist soil and leaf litter, with small sticks extending to the top of the jar. The jars were placed in natural light and temperature conditions. At intervals throughout the daylight hours, the numbers of beetles in the top five cm of the jar (i.e., near the top of the vertical stick) was counted. This experiment was repeated monthly for three months, in July, August and September. The mean results (Fig. 1) show that under conditions of natural light and temperature, and constant high humidity, there was a general early morning increase in locomotor activity or a tendency to climb, leading to a peak shortly before 10 a.m. EST. This agreed precisely with the field observations in corn fields. Furthermore, the time pattern agrees with that noted above when beetles move out from the aggregation to feed on nearby flower pollen.

The relationship between the effects of light, gravity and humidity was further investigated by measuring the vertical distribution of beetles in bell jars in constant light (3 K lux) and constant darkness after 12 or 36 hours of water deprivation, and again after the addition of water to the soil at the bottom of the containers. The results (Fig. 2) show that a) the beetles were distributed at higher levels in darkness than in light irrespective of their state of desiccation; and b) that, when desiccated, beetles kept in darkness were distributed at markedly lower levels than when they were supplied with water. However, this difference did not appear when water was added to desiccated beetles kept in constant light.

Discussion

It is known that *C. maculata* has a low tolerance for desiccation, and Ewert and Chiang (1965) have shown that the beetles move up a moisture

gradient and exhibit negative phototaxis. During extensive testing in an insect olfactometer, with many stimuli, we could find no evidence of chemotaxis, but confirmed that *C. maculata* could detect and move toward areas of high moisture level. This positive hygrotaxis appears to be the dominant factor in the behavior of the beetle. It plays an important role in the formation of aggregations (Benton and Crump 1979) and is a major influence in the distribution of beetles in their summer habitats. The importance of phototactic and geotactic elements in the distribution of the beetles are difficult to elucidate due to their changing nature and interaction. We have observed that *C. maculata* shows apparent positive phototaxis, probably complemented by a negative geotaxis, in order to effect dispersal from the overwintering site, the same individuals having shown the opposite response during the formation of the aggregation some months earlier. The same sort of shift occurs in summer between early morning and late morning. Avoidance of desiccation is of primary importance to this species, however, and it may well be that the aforementioned downward movement of late morning is the result of a positive hygrotaxis as the air around the upper strata of corn becomes drier. This would act to guide the beetles down toward the basal regions of the corn. Since a good deal of pollen accumulates in leaf axils and on the ground, this would permit pollen feeding to continue even though the beetles were relatively inactive. Considerable refinements of experiments are essential to eliminate all responses except the one being studied before we can understand the movements of this species, since responses appear to alter substantially with subtle changes in environmental conditions.

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State University College, Fredonia, New York 14063.

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PRINCIPAL COMPONENTS ANALYSIS OF BIOGEOGRAPHIC PATTERNS AMONG *HELICONIA* INSECT COMMUNITIES

Richard P. Seifert

Abstract.—This study explores biogeographic patterns among insect communities which live in the water-filled floral bracts of *Heliconia* plants. Twenty-five collections from 13 Neotropical locations are studied using a principal components analysis where the collections are ordinated on the basis of the frequency of occurrence of the 23 most common insect morpho species. *Heliconia* species from the French Antilles show a depauperate insect community, apparently due to island isolation. Floral structure is important in determining the insect community: *Heliconia* species with small floral bracts have low species richness and only one *Heliconia* species with a pendant inflorescence has an aquatic or semi-aquatic insect community. Different *Heliconia* species collected from the same location do not necessarily have comparable insect species communities.

Introduction

Biogeographic studies have held an important position in the growth and understanding of evolutionary ecology since the work of Darwin (1859) and Wallace (1876). These studies have attempted to discern patterns of distributions and to identify the factors which determine the distributions of either taxonomically or ecologically related organisms (Price 1975; Pianka 1978). This paper is a biogeographic study based on a principal components analysis (Pielou 1977) of collections of 25 different insect communities living in the water-filled floral bracts of *Heliconia* (Zingiberales: Musaceae) plants collected from 13 different locations in Costa Rica, northern South America and the Antilles made over a period of 8 years. Through this analysis I tried to discern basic biogeographic patterns of *Heliconia* insect communities, to determine if *Heliconia* species in the same location had similar insect communities even if they bloomed during different seasons and to determine if similar insect communities lived in the water-filled bracts of *Heliconia* species with similar bract morphologies.

Plants in the genus *Heliconia* are common members of low- and mid-elevation Neotropical wet forests. These plants are most frequent in sunlit areas. Detailed studies on the natural history of these plants have been published by Stiles (1975, 1979). Many *Heliconia* species have inflorescences consisting of a series of large erect cup like floral bracts, each bract containing several flowers (Fig. 1). The erect bracts collect and hold both rainwater and water actively pumped into the bracts by the plant (Seifert



Fig. 1. An inflorescence of *Heliconia* cf. *caribaea* sp. 2 from Limóncocha, Ecuador.

and Seifert 1976). A diverse group of insects live all or part of their lives in the water-filled *Heliconia* bracts (Seifert 1975; Seifert and Seifert 1976). The insect species composition varies with *Heliconia* species and depends in part on the flowering season of the *Heliconia* species as well as the proportion of the bract which has standing water (Seifert 1980). Some *Heliconia*

species have inflorescences which are pendant rather than erect. In most cases, the bracts of pendant species do not hold water or harbor an aquatic insect community. However, one pendant species (*H. rostrata* Ruiz and Pavon) has tightly compressed bracts which retain water and maintain a community of insects similar to that found in some erect bract *Heliconia* species.

Materials and Methods

Twenty-five *Heliconia* insect communities were collected from different *Heliconia* species from Costa Rica (2 locations), Venezuela (5 locations), Ecuador (3 locations), Trinidad (1 location), Martinique (1 location) and Guadeloupe (1 location) (Table 1). In 3 cases I collected insect communities from the same *Heliconia* species at the same location in both the early and late portions of the blooming season. At some sites I was able to make collections of more than 1 *Heliconia* species. In each collection I sampled at least 20 inflorescences, carefully dissected each bract and recorded the number of individuals of each insect species in each inflorescence. After all collections were made, I identified (to genus or family) the 23 insect "morpho species" found most commonly in the collections. For this study, insect morpho species were recorded as ecological equivalents. Thus, for example, there was a category for small hispine beetle (genus *Cephaloleia*) and I recorded this as present from several collections even though different hispine species existed at different locations. I assumed that the small hispines represented organisms foraging in the same manner even though their Latin binomens differed. Further, in the case of hispine beetles, I recorded adults and larvae separately since in some hispine species only the larvae feed on the inflorescences (Strong 1977a, b; Seifert and Seifert 1979). Next I computed the frequency of occurrence of each insect morpho species in each collection. This figure was simply the number of inflorescences which had at least one specimen of a given insect morpho species divided by the total number of inflorescences in the collection. Following this, a matrix of insect morpho species frequencies (columns) for each *Heliconia* collection (rows) was constructed (Table 2). These data were analyzed using a principal components analysis which examined the similarity of collections based on their insect morpho species frequencies (R technique of Pielou 1977).

Principal components analysis is an ordination method which is used to examine the pattern of variation among variates where no a priori patterns of causality are suggested. This technique shows relationships among samples which are not apparent from a simple inspection of the data. The original data are projected onto a plot (or series of plots) of few dimensions in such a way that the arrangement of points suffers the least possible distortion. Each principal component is a linear combination of the original vari-

Table 1. Collection label, *Heliconia* species resemblance, collection location and season of collection for 25 *Heliconia* collections used in the principle components analysis.

Collection label	<i>Heliconia</i> species resemblance and descriptor	Collection location	Approximate co-ordinates	Season collected
1	<i>aurea</i> Rodríguez	Rancho Grande Venezuela	10°21'N 65°41'W	wet season
2	cf. <i>humilis</i> sp. 1 Jacq.	La Escalera Venezuela	05°45'N 61°25'W	wet season
3	cf. <i>humilis</i> sp. 2 Jacq.	El Dorado Venezuela	06°41'N 61°35'W	wet season
4	cf. <i>caribaea</i> sp. 2 Lamarck	Limóncocha Ecuador	0°34'S 76°38'W	dry season
5	cf. <i>humilis</i> sp. 3 Jacq.	Primavera Ecuador	0°32'S 76°45'W	dry season
6	<i>episcopalis</i> Velloso	Primavera Ecuador	0°32'S 76°45'W	dry season
7	<i>bihai</i> Linn.	Les Nuages Martinique	14°42'N 61°06'W	wet season
8	cf. <i>caribaea</i> sp. 1 Lamarck	Panaquire Venezuela	10°21'N 66°15'W	wet season
9	<i>bihai</i> Linn.	Bains Juanes Guadeloupe	16°03'N 61°40'W	wet season
10	<i>caribaea</i> Lamarck	Les Nuages Martinique	14°42'N 61°06'W	wet season
11	<i>caribaea</i> Lamarck	Bains Juanes Guadeloupe	16°03'N 61°40'W	wet season
12	cf. <i>caribaea</i> sp. 1 Lamarck	La Trilla Venezuela	10°22'N 65°42'W	wet season
13	<i>rostrata</i> Ruiz and Pavon	Limóncocha Ecuador	0°34'S 76°38'W	dry season
14	<i>latispatha</i> Bentham	Tinalandia Ecuador	0°14'S 79°07'W	dry season
15	cf. <i>caribaea</i> sp. 1 Lamarck	Guatopo Venezuela	09°45'N 66°28'W	wet season
16	<i>rodriguensis</i> Aristeguieta	Guatopo Venezuela	09°45'N 66°28'W	wet season

Table 1. Continued.

Collection label	<i>Heliconia</i> species resemblance and describer	Collection location	Approximate co-ordinates	Season collected
17	<i>bihai</i> Linn.	Rancho Grande Venezuela	10°21'N 65°41'W	dry season (early)
18	<i>bihai</i> Linn.	Rancho Grande Venezuela	10°21'N 65°41'W	wet season (late)
19	<i>imbricata</i> (Kuntze) Baker	Rincón de Osa Costa Rica	08°42'N 83°30'W	wet season (early)
20	<i>imbricata</i> (Kuntze) Baker	Rincón de Osa Costa Rica	08°42'N 83°30'W	wet season (late)
21	<i>wagneriana</i> Petersen	Rincón de Osa Costa Rica	08°42'N 83°30'W	dry season (early)
22	<i>wagneriana</i> Petersen	Rincón de Osa Costa Rica	08°42'N 83°30'W	dry season (late)
23	<i>latispatha</i> Bentham	Sirena Costa Rica	08°40'N 83°40'W	dry season
24	<i>wagneriana</i> Petersen	Sirena Costa Rica	08°40'N 83°40'W	dry season
25	cf. <i>caribaea</i> sp. 1 Lamarck	Simla Trinidad	10°45'N 61°22'W	wet season

NOTE: The taxonomic status and nomenclature of many members of the genus *Heliconia* are uncertain. Identifications follow, when possible, Aristeguieta (1961) and Daniels and Stiles (1979). *Heliconia* species designated as *H. cf. caribaea* and *H. cf. humilis* represent morphological forms, some of which may be undescribed, which appear similar to members of the *H. caribaea* and *H. humilis* species complexes. However, only the forms from Martinique and Guadeloupe represent true populations of the species originally described as *H. caribaea* Lamarck.

ates where the first principal component accounts for the maximum possible variance and each subsequent component accounts for a decreasing amount of the residual variance. In this study each of the 25 *Heliconia* collections is characterized by the frequency of occurrence of the 23 morpho species. The *Heliconia* collections represent the variates to be ordinated; the insect morpho species frequencies are the attributes on which the ordination is based. Principal components analysis has been used frequently in taxonomic studies (Sneath and Sokal 1973) as well as in ecological studies (Pielou 1977). Often the characters used are standardized when the variates are measured in different units. However, in ecological work when the variates are measured in the same units (here, frequencies of insect morpho species) standardization is not appropriate (Pielou 1977). Further, some workers, partic-

Table 2. Frequency of occurrence of the 23 most common insect "morpho species" (listed by letters) found in 25 *Heliconia* inflorescences collections.

<i>Heliconia</i> collection label	Insect morpho species frequencies											
	a	b	c	d	e	f	g	h	i	j	k	l
1	0.91	0.14	0.84	0.02	0.28	0.97	0.14	0.00	0.22	0.09	0.03	0.02
2	0.85	0.40	0.35	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.05	0.00
3	1.00	0.55	0.10	0.65	0.15	0.00	0.00	0.00	0.00	0.05	0.00	0.05
4	0.79	0.88	0.09	0.02	0.21	0.40	0.26	0.54	0.37	0.26	0.09	0.00
5	0.77	0.60	0.00	0.13	0.57	0.10	0.43	0.27	0.00	0.13	0.00	0.00
6	0.00	0.61	0.00	0.00	0.79	0.03	0.00	0.00	0.00	0.00	0.00	0.00
7	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00
8	1.00	0.17	0.27	0.67	0.57	0.73	0.30	0.00	0.20	0.03	0.00	0.00
9	0.00	0.00	0.48	0.31	0.00	0.00	0.00	0.00	0.00	0.10	0.10	0.00
10	0.52	0.00	0.00	0.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	0.00	0.00	0.58	0.93	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
12	1.00	0.83	0.64	0.93	0.80	0.23	0.00	0.03	0.00	0.17	0.00	0.00
13	0.00	0.79	0.00	0.10	0.69	0.00	0.07	0.21	0.07	0.45	0.00	0.03
14	0.68	0.77	0.10	0.00	0.39	0.00	0.32	0.00	0.32	0.06	0.16	0.00
15	1.00	0.85	0.50	0.80	0.25	0.30	0.05	0.00	0.00	0.10	0.00	0.00
16	0.82	0.71	0.52	0.94	0.09	0.15	0.03	0.12	0.35	0.12	0.03	0.03
17	0.59	0.66	0.94	0.28	0.03	0.88	0.41	0.12	0.19	0.59	0.28	0.00
18	0.12	0.70	0.79	0.18	0.00	1.00	0.24	0.09	0.42	0.39	0.09	0.03
19	0.83	0.80	0.30	0.93	0.47	0.70	0.50	0.03	0.03	0.23	0.20	0.73
20	0.40	0.80	0.37	0.87	0.33	0.83	0.17	0.43	0.00	0.27	0.13	0.53
21	0.10	0.97	0.43	0.03	0.00	0.07	0.37	0.00	0.00	0.13	0.03	0.03
22	0.83	0.67	0.77	0.37	0.97	0.00	0.07	0.67	0.00	0.60	0.07	0.27
23	0.60	0.07	0.13	0.00	0.27	0.00	0.73	0.00	0.00	0.13	0.00	0.00
24	0.95	0.90	0.90	0.05	0.90	0.10	0.16	0.32	0.00	0.26	0.00	0.00
25	0.85	0.20	0.10	0.05	0.20	0.10	0.00	0.00	0.35	0.10	0.05	0.00

NOTE: The *Heliconia* collection labels are the same as those listed in Table 1. Insects represented by letters are: a = *Quichuana* (Syrphidae), b = *Gillissius* (Hydrophilidae), c = *copestylum* (Syrphidae), d = *Merosargus* (Stratiomyidae), e = *Beebeomyia* (Richardiidae), f = *Cephaloleia* larva (Chrysomelidae), g = *Cephaloleia* adult (Chrysomelidae), h = small *Gillissius* (Hydrophilidae), i = large hispine (Chrysomelidae), j = *Odontolinus* (Staphylinidae),

ularly in taxonomic studies, remove highly correlated characters. Once again this procedure is less commonly used in ecological work where high correlations of insect frequencies may indicate a particular and regular pattern of community structure. I have constructed a correlation matrix based on insect morpho species frequencies (Table 3). However, insect morpho species whose frequencies are highly correlated were not removed from the data set used to produce this principal components analysis. My procedure (no standardization, no removal of correlated characters) follows Pielou (1977) who can be referred to for a more detailed treatment of principal components analysis in ecological studies. Thus, the data set which I use in this principal components analysis is the *Heliconia* collection by insect morpho species frequencies listed in Table 2.

Table 2. Continued.

Heliconia collection label	Insect morpho species frequencies										
	m	n	o	p	q	r	s	t	u	v	w
1	0.00	0.00	0.02	0.00	0.00	0.00	0.00	1.00	1.00	0.57	0.00
2	0.05	0.00	0.00	0.00	0.15	0.00	0.00	0.55	0.00	0.00	0.00
3	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.20	0.00	0.40
4	0.02	0.00	0.16	0.00	0.19	0.02	0.09	0.59	0.00	0.00	0.00
5	0.03	0.00	0.00	0.00	0.07	0.00	0.03	0.90	0.00	0.00	0.00
6	0.03	0.06	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00
7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68	0.00	0.00
8	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.97	0.20	0.00	0.17
9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00
10	0.00	0.03	0.03	0.00	0.00	0.03	0.00	0.03	0.87	0.00	0.00
11	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	1.00	0.00	0.00
12	0.00	0.30	0.33	0.03	0.00	0.00	0.00	0.97	0.00	0.00	0.00
13	0.00	0.03	0.21	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
14	0.03	0.00	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
15	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.00	0.00
16	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.91	0.00	0.00	0.00
17	0.00	0.00	0.09	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
18	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
19	0.00	0.00	0.17	0.07	0.00	0.00	0.17	0.77	0.00	0.00	0.00
20	0.00	0.00	0.17	0.03	0.00	0.03	0.10	0.73	0.00	0.00	0.00
21	0.00	0.17	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
22	0.20	0.07	0.43	0.00	0.00	0.03	0.03	0.83	0.00	0.00	0.00
23	0.07	0.20	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24	0.00	0.21	0.05	0.00	0.05	0.00	0.21	0.73	0.79	0.00	0.00
25	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.15

k = *Carcinophora* (Carcinophoridae), l = cockroach (Blattidae), m = Noctuidae, n = Pyralidae, o = small Staphylinidae, p = tiny Staphylinidae, q = Scarabidae, r = Curculionidae, s = Carabidae, t = *Wyeomyia* (Culicidae), u = *Culex* (Culicidae), v = *Trichoprosopon* (Culicidae), w = *Toxorhynchites* (Culicidae).

Results

The first 3 components accounted for a total of 68.13% of the variation of *Heliconia* insect communities. The component weights for each of the first 3 components are listed in Table 4. Component 1 weights most heavily, in decreasing order of weight, on *Quichuana* (Diptera: Syrphidae), *Gillisia* (Coleoptera: Hydrophilidae) and *Wyeomyia* (Diptera: Culicidae). These are the most frequently encountered and abundant insect species in many *Heliconia* inflorescences. The frequencies of *Quichuana* and *Wyeomyia* are positively correlated in *Heliconia* collections (Table 3). Component 2 weighs most heavily on *Culex* (Diptera: Culicidae), *Merosargus* (Diptera: Stratiomyidae) (a negative weight) and *Copestylum* (Diptera: Syrphidae) (a negative weight). This component weighs most heavily on a second group

Table 3. Matrix of pairwise correlations among the frequencies of occurrence of 23 insect morpho species from 25 different *Heliconia* collections.

Insect morpho species	Insect morpho species											
	a	b	c	d	e	f	g	h	i	j	k	l
a	1.000											
b	0.306	1.000										
c	0.176	0.262	1.000									
d	0.197	0.077	0.139	1.000								
e	0.313	0.287	0.043	-0.071	1.000							
f	0.170	0.201	0.467	0.159	-0.104	1.000						
g	0.115	0.214	-0.023	-0.228	0.013	0.309	1.000					
h	0.142	0.466	0.172	-0.066	0.438	0.085	0.052	1.000				
i	0.154	0.153	0.103	-0.202	-0.247	0.420	0.098	0.046	1.000			
j	-0.015	0.518	0.485	-0.076	0.281	0.347	0.239	0.652	0.155	1.000		
k	-0.014	0.286	0.276	-0.010	-0.207	0.496	0.360	0.157	0.313	0.493	1.000	
l	0.080	0.301	0.042	0.418	0.189	0.361	0.238	0.308	-0.186	0.284	0.460	1.000
m	0.264	-0.084	-0.077	-0.261	0.302	-0.327	-0.062	0.368	0.039	0.236	-0.041	0.055
n	0.188	0.292	0.257	0.064	0.388	-0.258	0.105	-0.010	-0.313	0.036	-0.376	-0.166
o	0.160	0.259	0.004	-0.064	0.441	-0.108	0.397	0.368	-0.035	0.418	0.204	0.243
p	0.167	0.309	0.036	0.516	0.217	0.350	0.216	0.038	-0.199	0.106	0.378	0.843
q	0.246	0.205	-0.139	-0.351	0.016	-0.083	0.033	0.377	0.132	-0.042	0.002	-0.150
r	-0.294	0.148	-0.059	0.081	0.129	-0.001	-0.120	0.491	-0.086	0.578	0.139	0.157
s	0.070	0.289	0.036	-0.039	0.496	0.147	0.210	0.331	-0.180	0.082	0.090	0.462
t	0.788	0.278	0.221	0.305	0.440	0.282	-0.069	0.325	0.099	0.007	-0.136	0.281
u	-0.115	-0.497	0.180	0.092	-0.182	-0.035	-0.303	-0.193	-0.185	-0.325	-0.314	-0.205
v	0.179	-0.215	0.315	-0.196	-0.033	0.411	-0.033	0.125	0.170	-0.104	-0.055	-0.060
w	0.336	-0.108	-0.244	0.143	-0.073	-0.068	-0.168	-0.201	0.041	-0.225	-0.198	-0.077

of commonly encountered species all of which are mosquito and fly species. Component 3 weighs most heavily on insects associated with the first two components: *Copestylum* (a negative weight), *Gillsius* (a negative weight) and *Wyeomyia*.

The results of the principal components analysis are presented graphically in Figures 2, 3 and 4. Figure 2 shows a plot of component 1 versus component 2. The collections from the French Antilles (10, 7, 9, 11) are grouped in the lower left region of the graph. These collections have low insect species richness. In particular, hydrophilid, hispine and staphylinid beetles which are common members of many *Heliconia* insect communities, are not found in the island collections. Further, in 3 of the collections (7, 9, 11) only 1 genus of mosquito (*Culex*) was recorded, while up to 4 genera are sometimes found in mainland collections. On the right edge of the graph are collections (24, 12, 15, 8, 3) from various locations which, with the exception of *H. wagneriana* Petersen (24), have morphologies similar to *H. cf. caribaea* Lamarck (Fig. 1). This graph also shows close association of insect community structure among collections of the same *Heliconia* species from the same locations. Thus, both the early (17) and late (18) collections of *H. bihai* L. from Rancho Grande (Venezuela), the early (19) and late (20) collections of *H. imbricata* (Kuntze) Baker and Rincón de Osa (Costa Rica)

Table 3. Continued.

Insect morpho species	Insect morpho species										
	m	n	o	p	q	r	s	t	u	v	w
a											
b											
c											
d											
e											
f											
g											
h											
i											
j											
k											
l											
m	1.000										
n	-0.035	1.000									
o	0.385	0.375	1.000								
p	-0.180	0.104	0.249	1.000							
q	0.043	-0.123	-0.077	-0.133	1.000						
r	0.046	-0.187	0.264	-0.029	-0.006	1.000					
s	-0.121	0.166	-0.040	0.410	0.194	-0.092	1.000				
t	0.205	0.118	-0.013	0.324	0.197	-0.224	0.222	1.000			
u	-0.274	-0.077	-0.326	-0.197	-0.118	0.014	-0.005	-0.068	1.000		
v	-0.107	-0.126	-0.117	-0.071	-0.079	-0.114	-0.125	-0.289	0.474	1.000	
w	0.229	-0.203	-0.227	-0.114	-0.127	-0.184	-0.117	-0.187	-0.037	0.067	1.000

and the early (21) and late (22) collections of *H. wagneriana* from Rincón de Osa are located close to one another.

Considering Figure 3 next, which plots component 1 versus component 3, much of the same clustering as in Figure 2 is shown. *Heliconia* species which were collected twice from the same location cluster together, *Heliconia* species with morphologies similar to *H. cf. caribaea* cluster together and the Antillean collections border the left side of the graph. Here, however, the Antillean collections (10, 7, 11, 9) enclosed the collection of *H. episcopalis* Velloso from Primavera, Ecuador (6). *H. episcopalis* is a species with small floral bracts and contains few insects. Thus, the generation of low insect diversity *Heliconia* plants occurs both because of the isolation of some *Heliconia* species on islands and because of the small inflorescence size of *H. episcopalis*.

The final graph, Figure 4, which compares component 2 versus component 3, again shows groupings of the species from the Antilles, clustering of collections of the same *Heliconia* species collected at different times and clustering of *Heliconia* species with similar floral morphologies. Figure 4, however, also shows that *H. rostrata* from Limóncocha, Ecuador (13) lies on the right side of the graph rather distant from most other collections. *H. rostrata* represents the only *Heliconia* species studies which had pendant

Table 4. Component weights on 23 insect morpho species from 25 *Heliconia* collections.

Insect morpho species	Component number			
	1	2	3	4
a	0.667	-0.034	0.125	-0.049
b	0.546	0.097	-0.188	0.074
c	0.360	-0.128	-0.191	0.006
d	0.374	-0.245	0.031	0.011
e	0.340	0.083	0.056	0.204
f	0.270	-0.055	-0.167	-0.150
g	0.162	0.053	-0.065	0.002
h	0.126	0.042	-0.029	0.035
i	0.103	0.014	-0.034	-0.050
j	0.169	0.028	-0.114	0.037
k	0.052	-0.000	-0.044	-0.013
l	0.080	-0.001	-0.030	-0.013
m	0.027	0.011	0.016	0.006
n	0.052	0.005	-0.006	0.035
o	0.100	0.047	-0.017	0.056
p	0.007	-0.001	-0.002	-0.001
q	0.023	0.010	0.007	-0.003
r	0.008	-0.000	-0.006	0.007
s	0.037	0.007	-0.003	0.020
t	0.527	-0.039	0.142	-0.079
u	0.117	-0.290	0.039	0.113
v	0.020	-0.024	0.007	-0.018
w	0.035	-0.010	0.029	-0.015

NOTE: Insects listed by letters follow the same sequence as that listed in Table 2.

inflorescences but still contained an aquatic insect community. While this community includes many of the common insects, it is unusual in that neither syrphid fly genera nor hispine beetle larvae were represented in the collection.

Discussion

The principal components weigh heavily on some of the most common fly, mosquito and beetle species. This implies that much of the variation in these insect communities from the 25 *Heliconia* collections is dependent on differences in *Quichuana*, *Gillisia*, *Wyeomyia*, *Culex*, *Merosargus* and *Copestylum* frequencies. The resulting placement of the 25 *Heliconia* collections on the principal components analysis graphs (Figs. 2, 3, 4) can be interpreted in relationship to knowledge about *Heliconia* collection localities, bract morphologies and flowering phenologies. The principal components analysis shows most clearly the similarity of the depauperate fauna of *Heliconia* inflorescences from the Antilles. Low species richness among

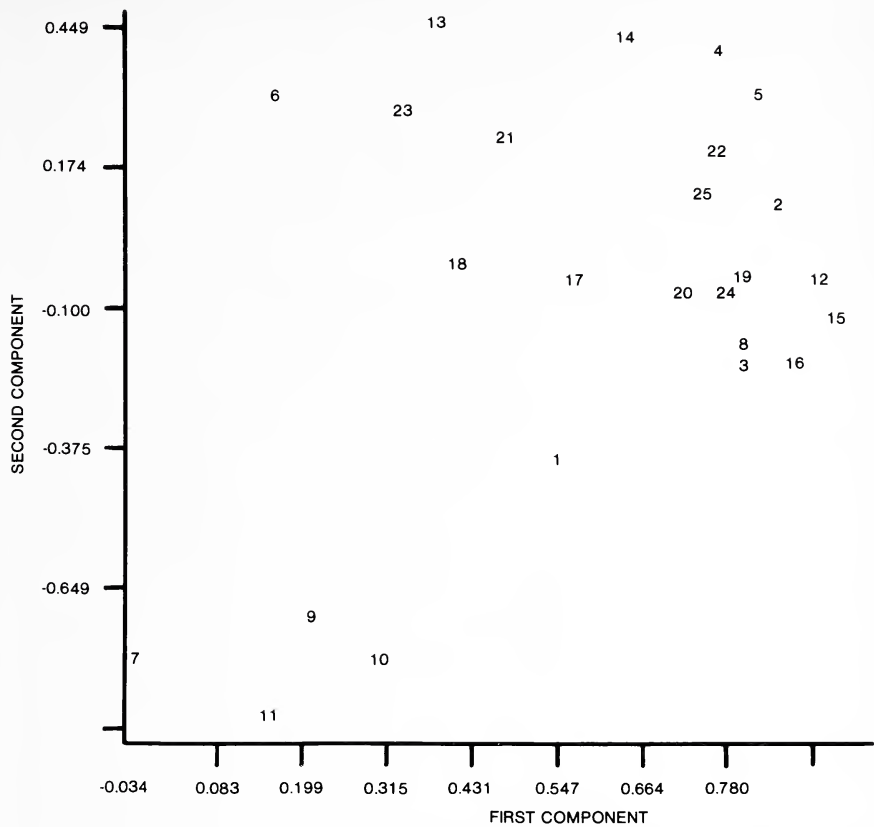


Fig. 2. A plot of component 1 versus component 2 for 25 collections of *Heliconia* insect communities. The numbers are the same as those listed in Table 1.

island biota is a commonly observed phenomenon (MacArthur and Wilson 1967; Carlquist 1974). In the case of *Heliconia* insect communities, this reduction of species richness is largely the result of a lack of beetle species and the presence of only 1, instead of several, mosquito species. I suspect that the lack of these insects is simply the result of an inability of some insects to locate, invade and colonize the islands. In Guadeloupe I was able to maintain Ecuadorian hispine species in petri dishes by feeding them bracts of both *H. bihai* Linn. and *H. caribaea* from local *Heliconia* populations. Thus, it seems clear that these beetles could form a breeding population on Guadeloupe. That they have not done so is probably attributable to their low rates of movement. Other research (Beaman 1980) has shown that *Heliconia* feeding hispines move only short distances among *Heliconia* clumps and do not exhibit long range dispersal.

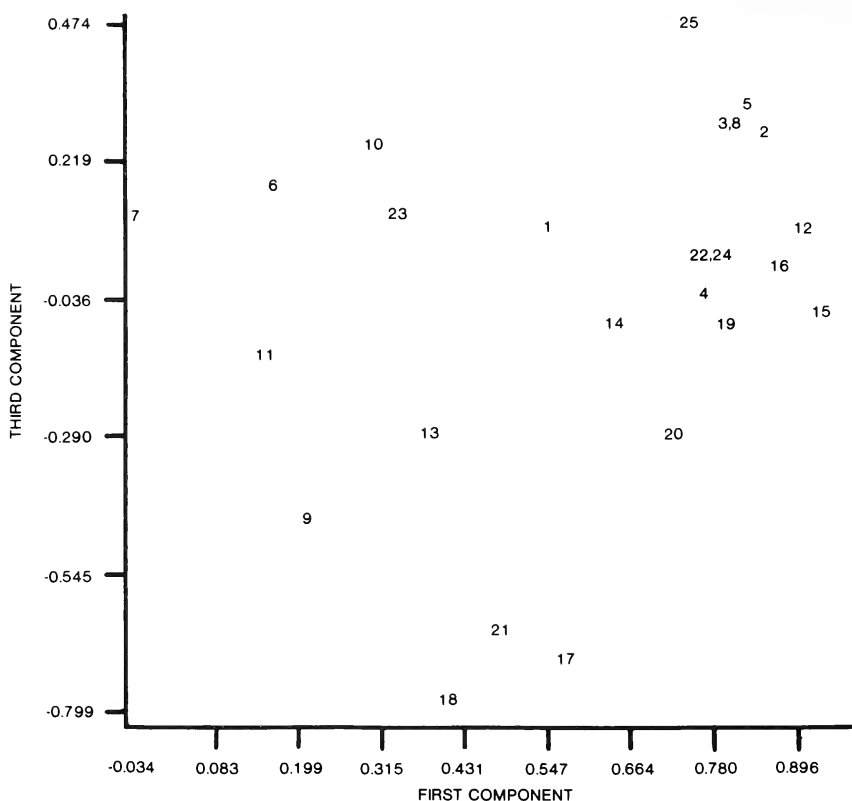


Fig. 3. A plot of component 1 versus component 3 for 25 collections of *Heliconia* insect communities. The numbers are the same as those listed in Table 1.

Further, from this biogeographic work we can interpret that floral morphologies are important in generating particular *Heliconia* insect community structure. Small *Heliconia* species, such as *H. episcopalis*, not only have low species richness but also are devoid of some of the most frequent *Heliconia* inquilines, syrphid fly larvae. Clearly, the kind of floral morphology of pendant *Heliconia* species is also important in determining the *Heliconia* insect community. While most pendant species do not contain an aquatic insect community (Seifert and Seifert 1979; personal observation), *H. rostrata*, because of its compressed bracts, does contain water and harbors some of the insect species associated with other *Heliconia* species. Finally, *Heliconia* with similar morphologies, such as *H. cf. caribaea* species, may contain largely similar *Heliconia* insect communities.

The results of the principal components analysis also point out that *Heliconia* inflorescences of the same species at the same location have similar *Heliconia* insect communities even if they are collected during different portions of the blooming season. The insect community structure, based on

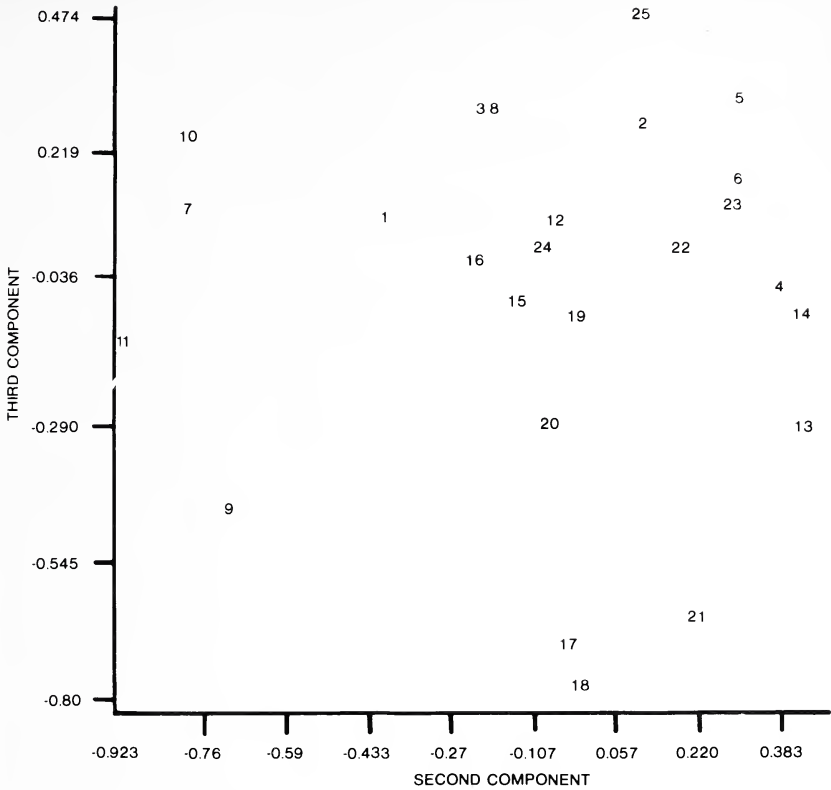


Fig. 4. A plot of component 2 versus component 3 for 25 collections of *Heliconia* insect communities. The numbers are the same as those listed in Table 1.

the presence of at least one individual of each insect species, remains approximately the same throughout much of the blooming season of a *Heliconia* species.

This principal components analysis did not show clustering of different *Heliconia* species from the same location. Thus, *H. aurea* Rodriguez from Rancho Grande (1) did not cluster close to *H. bihai* from Rancho Grande (17, 18), and *H. imbricata* from Rincón de Osa (19, 20) did not cluster with *H. wagneriana* from the same location (21, 22). Only in the cases of the collections from the Antilles, where isolation is important in determining insect species richness, did different *Heliconia* species from the same location show affinities.

In conclusion, this study has shown how principal components analysis can be used to examine the similarity of insect communities living in association with different species of closely related plants from different locations. The results of the analysis indicate the importance of plant isolation and floral morphology in determining insect community structure.

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Department of Biological Sciences, The George Washington University, Washington, D.C. 20052.

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NOTES ON SEASONALITY AND HABITAT ASSOCIATIONS OF
TROPICAL CICADAS (HOMOPTERA: CICADIDAE) IN
PREMONTANE AND MONTANE TROPICAL MOIST
FORESTS IN COSTA RICA

Allen M. Young

Abstract—Annual patterns of adult emergences and habitat associations for several species of tropical cicadas (Homoptera: Cicadidae) were studied within the premontane-to-montane tropical moist forest zone northwesterly of the Meseta Centrale region of Costa Rica. The region largely consists of expansive coffee plantations, secondary vegetation, and strips of forest along streams, and the censusing of cicadas at four widely separated localities (Grecia, Naranjo, San Ramon, and Esparta) covered an elevational range of about 200–1,100 meters. Coffee plantations in this region have an overstory (shade cover) of *Inga* spp. trees (Leguminosae) and sometimes (Grecia) a mixture of these trees with another legume tree, *Zygia longifolia*. *Z. longifolia* is also the dominant tree in forest remnants along streams in this region. Given the pronounced patterns of annual seasonal precipitation at all four localities and the mosaic of secondary coffee plantations and forest remnants at three of them, and forest remnants and secondary vegetation at the fourth (Esparta), it was expected that the census of nymphal skins and adult cicadas would indicate distinctive seasonal adult emergence cycles and habitat associations. The data confirmed this. *Fidicina amoena* emerges during the dry season near stream-edge *Zygia* trees in coffee plantations (Grecia) and near other legume trees in forest remnants (Esparta). *Fidicina semilata* and *F. "coffea"* emerge near *Inga* trees in coffee plantations (Naranjo and San Ramon) during the dry season as does *F. pronoe* and *F. spinocosta* in secondary vegetation (Esparta). *Fidicina mannifera* emerges during the wet season in primary forest remnants at about 200 meters elevation (Esparta). *Zammara smaragdula* emerges in the wet season near *Zygia* trees in coffee plantations (Grecia) and forest remnants along streams (Naranjo and San Ramon) and *Conibosa* sp. emerges during the wet season in coffee plantations (Grecia, Naranjo, and San Ramon). *Quesada gigas* emerges during the dry season near *Zygia* trees along the borders of coffee plantations and in stream-edge forest remnants. The data are discussed from the standpoint of adaptations in tropical cicadas to seasonality and habitats, the latter particularly in terms of the exploitation of legume trees as feeding sites (root crowns) of nymphs.

Introduction

A field survey of the cicadas across northern Costa Rica, extending from lowland tropical wet forest into montane wet forest, montane moist forest

and into lowland tropical dry forest, revealed distinctive distributional patterns for many genera and species (Young 1976). Such a transect slices through a series of distinctive climatic and vegetation zones (Holdridge et al. 1971) and varying degrees of seasonality in terms of the length and severeness of the dry season (Janzen 1967). Several previous studies have revealed that tropical cicadas may exhibit very pronounced adult seasonal emergences annually, and that genera and species sometimes also partition the local environment by habitat (Young 1972, 1974, 1975, 1980a, b, 1981a). These studies were conducted for the common genera and species found in these regions of Costa Rica: lowland tropical wet forest, premontane tropical wet forest, highland moist forest, and lowland tropical dry forest. The purpose of the present paper is to summarize the annual peak adult emergence periods and habitat associations for several genera and species of tropical cicadas in yet another major climatic belt of northern Costa Rica, the premontane-to-montane tropical moist forest zone. The data, although discontinuous, indicate that some cicadas of this zone emerge during the lengthy dry season, others during the wet season, and that most species are differentially associated with (a) forest remnants forming the borders of coffee plantations and grazing pastures, (b) shade trees in coffee plantations, and (c) secondary vegetation. The data are consistent with observations on cicada emergences at other sites in Costa Rica in that emergences are strikingly seasonal, and that a variety of habitats, including agricultural ones, are exploited by cicadas in the tropics.

Materials and Methods

I examined the temporal and spatial properties of adult emergences of cicadas by selecting four widely separated localities along the northwest axis through the highlands and adjacent mountains northwest of the Meseta Centrale region of Costa Rica: habitats located at the cities of Rosario de Grecia (Grecia), Naranjo, San Ramon, and Esparta, sites within Alajuela and Puntarenas Provinces (Fig. 1). This transect covers an elevational gradient from 825 meters (Grecia), 1042 meters (Naranjo), 1116 meters (San Ramon) down to 208 meters (Esparta). The first three localities are very similar topographically and floristically, consisting of rolling hills covered with extensive coffee plantations at least 100 years old in most parts, and with strips or remnants of forest vegetation along streams and rivers (Figs. 2, 3, 4). The coffee plantations have an overstory of primarily *Inga* spp. trees (Leguminosae) (Figs. 2, 3) and the forest remnants consist chiefly of adult-size *Zygia longifolia* trees (Leguminosae) (Fig. 4). The coffee plantation at Rosario de Grecia consisted of adult-size *Zygia* trees along streams and drainage ditches running through the plantings, and *Inga* trees as shade on slopes. Patches of grasslands are interspersed with the coffee agricultural



Fig. 1. The distribution of localities within the premontane-to-montane tropical moist forest zone in Costa Rica, northwest of the Meseta Centrale and San Jose, used to study cicada emergences. These localities are: (1) Grecia, (2) Naranjo, (3) San Ramon, and (4) Esparta.

system of the region. The fourth site, Esparta, is a very steep (incline about 60° in most places) forested ravine surrounded by patches of secondary growth and open pastures lightly to heavily grazed by *Brahma* cattle (Fig. 5). In this forest bordering a stream system, several genera of legume trees predominate, of which *Pithecollobium* species predominates. A marked dry season, of similar duration and severeness, is a major component of the climatic regime of all four sites (Fig. 6). Areas within each habitat studied at each locality are representative of the habitats in general.

A cicada census program was deployed at these four localities to test the hypothesis that representative cicada species at each one exhibit distinct annual emergence patterns somehow related to the annual seasonal cycle of precipitation (Fig. 6). A second hypothesis examined, also in a preliminary fashion, was that cicada emergences occur in different kinds of habitats at each locality, habitats that are representative of each locality overall. As with previous similar studies (Young 1972, 1974, 1975, 1980a, b, 1981a) cicada emergence patterns were studied by making collections of freshly



Fig. 2. The overstory of *Inga* spp. trees in the coffee plantation at Naranjo where emergences of *Fidicina semilata* and *Conibosa* sp. were studied. These shade trees, easily recognizable by the whitish bark, are rather uniformly distributed over large areas of the plantations in this locality.

discarded nymphal skins from marked plots in different habitats at each locality. The skins were collected, identified in the field to species, sexed, and counted every time a census was made. Whenever possible, adult specimens were also collected for voucher material to confirm species determinations later. Sample plots for collecting nymphal skins were usually 5×6 meters and in coffee plantations, about half were enclosing one *Inga* shade tree and the others only coffee bushes. Plots with shade trees also have coffee bushes, and the DBH for the shade trees is 20–35 cm. Nymphal skins were collected exhaustively from tree trunks, bushes, leaf litter, and ground surface. For most species, skins are readily identified to species based on gross morphological features (size, form, coloration). The reliability of species determinations of skins in this manner has been discussed elsewhere (Young 1980a). Because skins remaining from a previous year's emergence period are very discolored, broken, and crumbly, they are readily distinguished from fresh skins of the current emergence thereby eliminating a bias



Fig. 3. *Inga* spp. shade trees interspersed with coffee bushes in a plantation at San Ramon. Cicada nymphal skins were collected from the ground litter, coffee bushes, and trunks of shade trees, and special care was taken to examine branches cut away as part of pruning of coffee bushes as shown here.

of confusing two or more annual emergence periods. Records were also kept for adult cicadas heard or seen at times when nymphal skins were censused.

For the Rosario de Grecia locality the study plots were situated within two areas of a large coffee plantation, the selection of the plots being based on previous observations of nymphal skins in them. Prior visits to all four localities indicated that at least two large-bodied species of cicadas were active at each one. The Grecia coffee plantation has a mixed shade cover of *Z. longifolia* and *Inga* spp. trees, while the Naranjo and San Ramon plantations have several species of *Inga* trees as shade. In addition to setting up sample plots in coffee in Naranjo and San Ramon, I also established a large study plot along a forest remnant in San Ramon, adjacent to a coffee plantation. *Z. longifolia* is the only tree species in this plot. At Esparta, cicada nymphal skin distributions were examined by selecting plots around some adult-size legume trees where skins had been seen. Details of the sizes



Fig. 4. Stream-edge habitat near San Ramon showing a large *Zygia longifolia* tree (on right bank of stream), a typical emergence spot for cicadas such as *Zammaria smaragdula*.

of plots, total areas represented by sample sites, and census dates are summarized along with the data. The census program spanned a period of about two years and included samples taken in both wet and dry seasons.

Because my samples of nymphal skins are very discontinuous over each year of the study, one source of error in estimating density of emerging cicadas from my census program is the possibility that some nymphal skins were blown into the plots from other areas of the habitats studied, although more than 80% of the skins collected from all plots throughout the study were found attached to vegetation. Unlike some temperate zone cicadas, clean emergence holes are not commonly found in tropical species.

Results

The cicadas associated with each locality are shown in Figures 7 and 8 and can be described further as follows:

(A) GRECIA: *Fidicina amoena* • medium to large-bodied cicada (body



Fig. 5. An overview of the canopy of the primary forest remnant in the steep ravines at Esparta during the dry season. There are also surrounding patches of secondary vegetation in addition to pastures. The sides of the ravines with forest are steep (45–60°).

length 30 mm), greenish body all over, clear wings, bell-like chirp for courtship song. Also found at Naranjo, San Ramon, and Esparta, although not abundant. Common in some parts of the Meseta Centrale (Young 1980a), but not common in lowland and premontane tropical rain forest (Young 1972, 1980b). Probably scarce in lowland tropical dry forest, although a population occurs at Santa Rosa National Park (Young 1981a).

Zammara smaragdula • medium-sized cicada (body length 25 mm), distinctly mottled green and black body all over, bright green in male, more olive green in female; wings clear but with large black spots; “hoarse buzz” for courtship song. Also found at other localities mentioned above for *F. amoena* but excluding tropical rain forest sites in the northeast where it is replaced by *Z. smaragdina*; also found at Finca La Taboga, near Canas in lowland Guanacaste Province as well as at the Barranca Forest site (Young 1981a).

Quesada gigas • large-bodied cicada (44 mm), body all over streaked in shades of brown, olive green, and black; clear wings; very distinctive “lo-

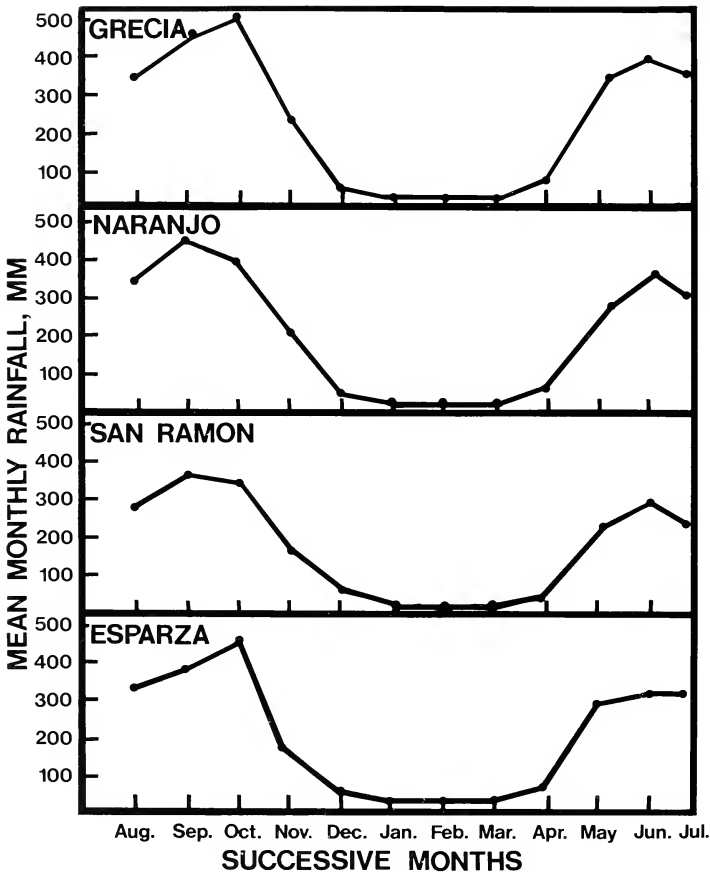


Fig. 6. The distribution of precipitation at the four localities within the premontane-to-montane tropical moist forest zone, showing a distinct and similar dry season between December and April for all localities. Data are means for the period 1943–1973. The standard deviations and coefficients of variation for monthly mean values are strikingly similar among all four localities, as expected for the very similar mean values for each month among all localities. Data is courtesy of the Meteorology Service of Costa Rica.

comotive whistle"-like courtship song, sometimes sings at dusk as do the others mentioned here but to lesser degree; widely-distributed throughout Costa Rica (Young 1976, 1980a, b).

Conibosa sp. • small-bodied cicada (10 mm) not figured in this paper, but with greenish head and thorax and maroon-colored abdomen and clear wings; courtship song resembles "zzzst" repeated over and over; widely distributed in the Meseta Centrale north of San Jose, and through the three coffee-growing localities discussed in this paper (see also Young 1980a), but not found to my knowledge in lowland to premontane tropical wet and dry

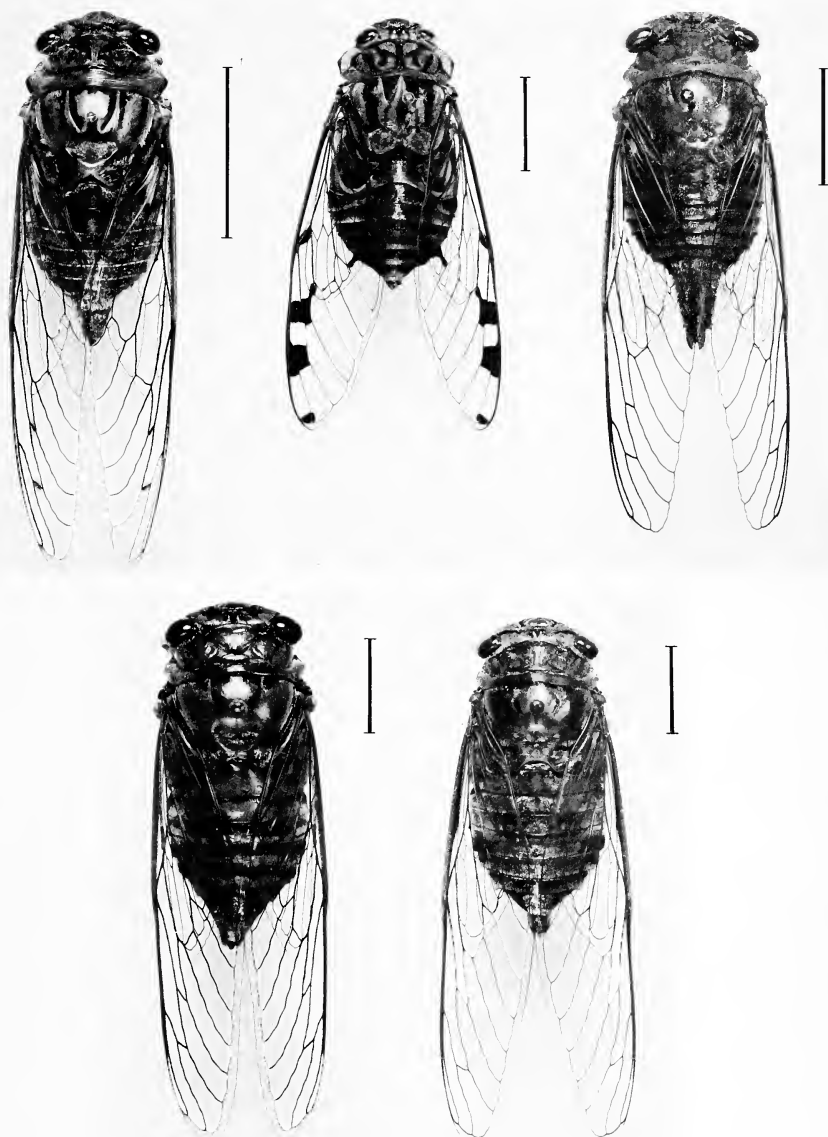


Fig. 7. Cicadas from the montane tropical moist forest zone in Costa Rica, northwest of the Meseta Centrale. Top row, left to right: *Quesada gigas*, *Zammara smaragdula*, and *Fidicina amoena*, three of the four common cicadas associated with predominantly coffee \times *Zygia* tree plantations in the Meseta Centrale, and lower montane moist forest region adjacent to it; Bottom row, left to right: *Fidicina semilata* and *Fidicina* "coffea," two of three common cicadas associated primarily with coffee \times *Inga* tree plantations in the upper montane moist forest region. In both series, the cicada not shown is the small *Conibosa* sp., but it is figured in Young (1980a).

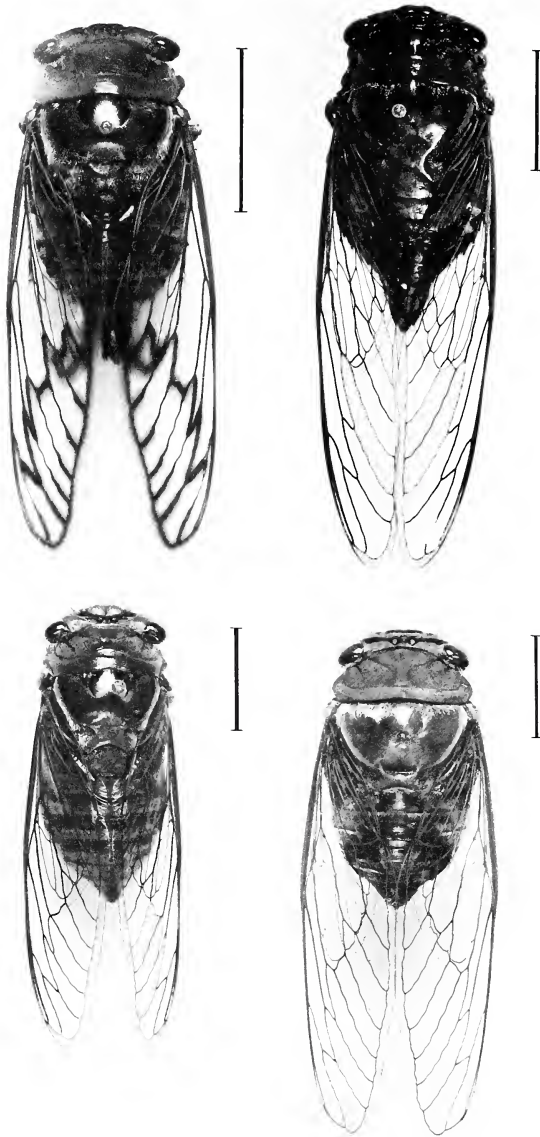


Fig. 8. Cicadas from the premontane tropical moist forest zone in Costa Rica, northwest of the Meseta Centrale. Top row, left to right: *Fidicina mannifera* and *Fidicina sericans*, two of four common primary forest species. Bottom, left to right: *Fidicina pronoe* and *Fidicina spinocosta*, the two common species associated with certain types of secondary vegetation in this region. The third common primary forest species of this region is *Zammara smaragdula*, figured in Fig. 7. For both Fig. 7 and 8, the vertical black line to the right of each cicada shown gives the actual body length relative to the magnified figure. See text for actual body length measures.

forest sites in Costa Rica. Appears to be distinctly associated with coffee plantations, perhaps more so than other cicadas.

(B) NARANJO: *Fidicina semilata* • species determination tentative as it may be a new species also tentatively called *F. "guayabana"* by A. M. Young and T. E. Moore; medium-sized cicada (body length 22 mm) with body generally greenish all over and wings crystal-clear; monotonous buzz-like courtship song and sings in coffee bushes and shade trees in coffee plantations; as to my knowledge found only at San Ramon in Costa Rica in addition to Naranjo.

(C) SAN RAMON: *Fidicina "coffea"* • probably a new species, tentatively determined by A. M. Young and T. E. Moore; medium-sized cicada (body length 23 mm), greenish but with some mottling (faint and thin) in brown, similar to *F. semilata* but with very distinctive courtship song consisting of pulsating buzz from coffee bushes and shade trees in plantations; not collected from other localities in Costa Rica; along with *F. semilata* appears somewhat restricted to the coffee habitat between Naranjo and San Ramon. May occur at Naranjo but not found.

(D) ESPARTA: *Fidicina mannifera* • large-bodied cicada (42 mm body length), dark brown with some mottling in green, particularly on prothorax dorsum; wings clear but with somewhat diffuse brown tinges along veins; very distinctive strong pulsating buzz, particularly at dusk; sings from trunks of large forest trees; widely distributed in northern Costa Rica outside of the Meseta Centrale and adjacent foothills (see Young 1972, 1976, 1980a, b).

Fidicina pronoe • medium-sized cicada (body length 25 mm) with cocoa-brown meso- and meta-thoracic dorsum and greenish head and prothoracic dorsum and lateral borders of meso- and meta-thoracic dorsum lined with white; wings clear and abdomen thickly banded laterally with black and brown; courtship song a high pulsating whistle heard mostly in open secondary vegetation where the canopy height is less than 7 meters; widely-distributed across northern Costa Rica (Young 1976, 1980b) and probably occurring at at least Naranjo and Grecia localities in the present study although most likely patchy and scarce as it is in the Meseta Centrale (Young 1980a). Probably not found in most localities in lowland tropical dry forest in Costa Rica but perhaps in Santa Rosa National Park (Young 1981a).

Fidicina spinocosta • at lower end of medium-sized range (body length 20 mm), body with head and thoracic areas bright green and abdomen maroon with silvery pubescence; body short and thick relative to other *Fidicinas* and wing length; wings crystal clear; courtship song is strongly pulsating short whistles mostly at dusk and from thick secondary vegetation; to my knowledge only occurs at this locality and also in the premontane tropical wet forest zone in the northeast (Young 1980a).

Fidicina sericans • large-bodied cicada (body length 30 mm) with black

Table 1. Notes on the seasonal distribution of adult cicadas along a transect through the Cordillera Central northwest of San Jose, San Jose Province, Costa Rica.

	Localities* where heard/ seen	Dry season dates areas examined	Wet season dates areas examined	Season of highest adult activity	Adult habitats	Habitats of nymphal skins
<i>Fidicina amoena</i>	RG, N, E	RG: II-12, 13; III-8; IV-16; V-10, 1973	RG: VII-21, 23; VIII- 20, 1973; VIII-29-74	dry	river-edge forest remnants, shade trees in coffee plantations	same
<i>F. semilata</i> **	N, SR	N: XII-29-31, 1972; I-11; II-11, 12; IV- 17, 27-28, 1973	N: VII-27-73	dry	shade trees in coffee plantations	same
<i>F. coffea</i> **	N, SR	SR: I-6-9; II-7-8, 1973	SR: VII-27-73; VII- 13-74	dry	shade trees in coffee plantations	
<i>F. pronoe</i> and <i>F. spinosa</i> <i>costa</i>	E	E: I-10; II-22; III-3, 17-19; IV-14-1973	E: VII-6-7, 13, 1974	dry (late)	secondary growth trees on hills; river-edge forest	same
<i>F. sericans</i>	E	Total dry season dates: 20	Total wet season dates: 7	dry	river-edge forest remnants in ravines	same
<i>F. mannifera</i>	E			wet	river-edge forest remnants in ravines	
<i>Zannara smaragdula</i>	RG, N, SR, E			wet	river-edge forest remnants	same
<i>Quesada gigas</i>	RG, N, E			dry (late)	river-edge forest remnants	same
<i>Conibosa</i> sp.	RG, N, SR			wet	shade trees and cof- fee bushes in coffee plantations	
<i>Pacarina</i> sp.	SR, E			dry	open fields and young secondary growth	same

* The localities examined are: Rosaria de Grecia (RG), Naranjo (N), Esparta (E), San Ramon (SR).

** Species designations unconfirmed due to lack of information on genus *Fidicina* in general. *Fidicina semilata* is also coded as *F. "guayabana"* in MPM and UWMZ Collections, and *F. "coffea"* is a temporary designation.

body mottled with dark green; wings slightly smokey with tinges of brown; courtship song a steady buzz; associated with primary and advanced secondary wet to moist forest habitats in northeast premontane, lower montane, and lowlands with nymphal skins invariably found near adult-size canopy legume tree species (Young 1972, 1980b, unpublished).

Another small-bodied cicada, *Pacarina* spp., also occurs at Esparta and perhaps at San Ramon, where they are associated with grassland habitats (Young 1974) but these species were not studied here. A summary of the distributions, localities, habitats or adult cicadas and nymphal skins, are given for these species in Table 1.

As shown in Table 1, forms such as *F. amoena*, *F. "coffea,"* *F. semilata* *F. sericans*, and *F. pronoe* are active in the dry season at their respective localities and many of these species occur in coffee plantations and other disturbed habitats. *Z. smaragdula* is the common wet season cicada at several localities and it is associated with forest remnants, places where its nymphal skins are found beneath *Zygia* trees. There is considerable overlap for some species of *Fidicina* (those associated with coffee plantations) among several coffee-growing localities and *Z. smaragdula* is found at all localities studied (Table 2). Forest-associated *Fidicinas* are restricted to Esparta (Table 2). Although the data on emergences are discontinuous, peak numbers of nymphal skins for several species censused agree with seasonal activity patterns as seen from adults (Fig. 9). Densities of nymphal skins generally fall well below one nymphal skin per square meter, although censuses of the same species at different sites within a locality generate great differences in estimates of density (Table 3). In coffee plantations at Naranjo and San Ramon, the greatest abundances of nymphal skins of *F. semilata* and *F. "coffea"* occur in plots with *Inga* spp. shade trees (one tree per plot) and plots with only coffee bushes beyond the immediate vicinity of shade trees disclose few skins (Table 4).

Density estimates for cicada nymphal skins will be very sensitive to areas involved, particularly when data from two or more sites are polled when individual sample sizes are low. Yet for a species such as *F. semilata*, the low estimate of about 0.12 nymphal skins per square meter may be biologically significant as suggested by the rather continuous data on nymphal skins of this cicada obtained from a small patch of coffee (840 m²) within the city of Naranjo for the period 30 December 1972 through 28 April 1973, a time span covering the major portion of the emergence period of this species at this locality. A total of 97 fresh skins were collected from this coffee patch, which contained a living (freshly-cut) stump of an *Inga* tree (DBH-25 cm) and about 50 coffee bushes giving a density estimate of about 0.12 skins per square meter. More than 70% of the skins collected were located within a 3-meter radius of the tree stump. The wood of the stump was still fresh and green as the tree had been cut down about a month before my census was commenced.

Table 2. The distribution of cicada species in the Central Cordillera northwest of San Jose, in Costa Rica, based on records of adults and nymphal skins.

Cicada	Localities			
	Rosaria de Grecia (coffee farms)	Naranjo (coffee farms)	San Ramon (coffee farms)	Esparta (forested ravines; second growth)
<i>Zammara smaragdula</i>	+	+	+	+
<i>Quesada gigas</i>	+	?	?	+
<i>Conibosa</i> sp.	+	+	+	
<i>Fidicina amoena</i>	+	+	+	
<i>F. semilata</i>	+	+	+	
<i>F. "coffea"</i>		+	+	
<i>F. pronoe</i>				+
<i>F. spinocosta</i>				+
<i>F. mannifera</i>				+
<i>F. sericans</i>				+
<i>Pacarina</i> sp.			+	+

There is some evidence of habitat partitioning at Rosaria de Grecia in terms of cicadas associated with *Zygia* trees: *F. amoena*, *Z. smaragdula*, and *Q. gigas* all emerge near these trees but not at other trees used as shade here. Furthermore, *Z. smaragdula* exhibits a tendency to emerge close to streams: of 174 nymphal skins of this cicada collected on 23 July 1973 along five parallel rows of coffee bushes running along a stream bordered with

Table 3. Abundance and densities of nymphal skins of cicadas from study plots at several localities in the Central Cordillera of Costa Rica (1973).

Cicada species	Localities studied	Habitat studied	Total area examined	Number of sites	Densities of nymphal skins
<i>Fidicina amoena</i>	Rosaria de Grecia	coffee plantation	2,030 m ²	2	0.17, 0.27/m ²
<i>Fidicina semilata</i>	Naranjo	coffee plantation	1,256 m ²	2	0.12, 0.40/m ²
	San Ramon	coffee plantation; riveredge forest remnant	1,128 m ²	2	0.12, 0.28/m ²
<i>Fidicina "coffea"</i>	San Ramon	coffee plantation; riveredge forest remnant	1,128 m ²	2	0.08, 0.28/m ²
<i>Zammara smaragdula</i>	Rosario de Grecia	coffee plantation	2,030 m ²	2	0.30, 0.42/m ²
<i>Conibosa</i> sp.	Rosario de Grecia	coffee plantation	2,030 m ²	2	0.06, 1.61/m ²
	San Ramon	coffee plantation; riveredge forest remnant	688 m ²	2	0.41, 0.78/m ²

Table 4. Collections* of nymphal skins of *Fidicina* spp. cicadas proximal and distal to *Inga* spp. shade trees in coffee plantations at Naranjo and San Ramon in the central highlands of Costa Rica northwest of the Meseta Centrale.

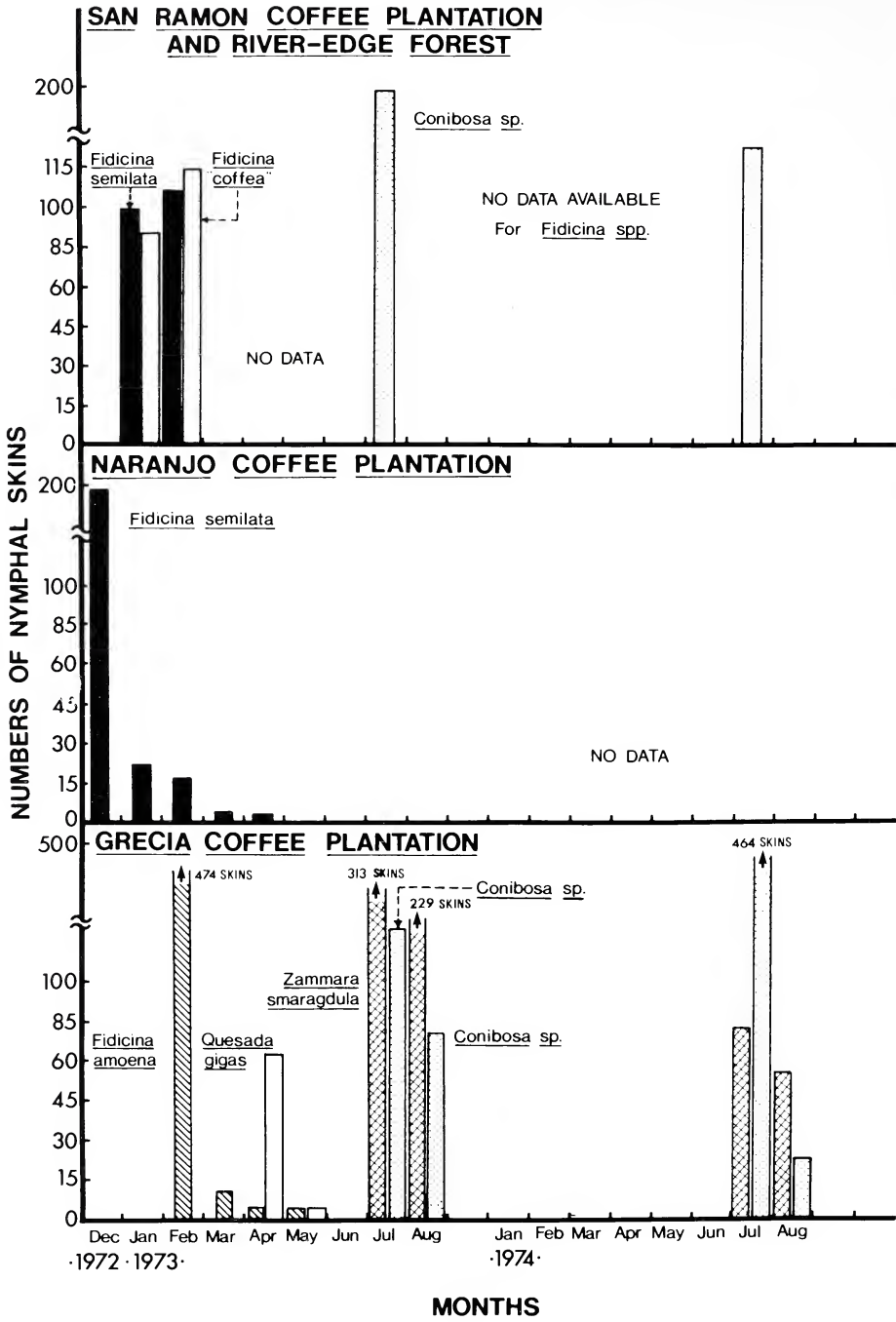
No. Inga trees** censused	DBH range	Tree trunks	Range trunk	Coffee bushes within 16 m² area (proximal)	Coffee bushes beyond 16 m² area (distal)	Ground (Inga trees + coffee)	Total nymphal skins		
							oo	oo	T
Naranjo: <i>Fidicina semilata</i>									
26	25–35 cm	35	0–12	108	5	12	93	67	160
San Ramon: <i>Fidicina semilata</i>									
33	25–35 cm	23	0–2	127	8	11	87	59	146
<i>Fidicina</i> “ <i>coffea</i> ”									
33	25–35 cm	16	0–2	23	2	10	22	19	41

* Over 60% of the shade trees sampled were *I. aff. fissicalyx* and the remaining ones were *I. goldmannii* and *I. leptoloba*.
** Census dates for Naranjo: 29 December 1972, 11 February 1973, 17 & 28 April 1973; census dates for San Ramon: 6–9 January 1973, 7 February 1973.

Zygia, 100 skins were taken from the row of bushes nearest to the stream, and with a marked decline in other rows, with none being found in the fourth and fifth rows away from the stream. In areas of coffee at Grecia where *Inga* trees are mixed with *Zygia* for shade, nymphal skins of *Q. gigas* are found beneath both kinds of trees.

In one stream-edge plot (600 m²) containing six large *Zygia* trees and 25 coffee bushes on a steep incline of about 50°, two census dates (6 January and 7 February 1973) disclosed 69 fresh skins of *F. semilata* and 100 fresh skins of *F. “coffea”* with the distributions of the skins of the two species mixed within the plot but not measured. These data and the accompanying estimates of density (0.12 for *semilata* and 0.28 for “*coffea*”) suggest co-occurrence of both species over a relatively small portion of the coffee plantation-border transitional habitat. Nymphal skins of these species are also mixed under *Inga* spp. trees in upland coffee, usually with 1–2 skins of each species per tree. Although my samples are small, the data suggest that *Z. smaragdula* is associated with *Zygia* trees only in the context that at both the Rosario de Grecia coffee habitat and San Ramon stream-edge habitat, nymphal skins of this species are found beneath *Zygia* trees. When *Inga* is used as a shade of upland coffee, only nymphal skins of *F. semilata* and *F. “coffea”* and *Conibosa* sp. are found near these trees, but not those of *Z. smaragdula*. Likewise, although *Fidicina*s are commonly found beneath *Inga* shade trees and even near the borders of *Zygia* with coffee, most *Zygia* habitats lack *Fidicina* nymphal skins.

The habitat complex of narrow valley strips of primary forest and adjacent patches of hillside secondary vegetation interspersed with grasslands at Es-



parta (Fig. 5) is characterized by rather low density emergences of cicadas, some, such as *F. pronoe* and *F. spinocosta* associated with secondary vegetation and others such as *F. mannifera*, *F. sericans* and *F. amoena* associated with primary forest. In one approximately 210 m² primary forest plot containing one canopy-like *Pithecollobium* tree censused once in the dry season (10 January 1973), fresh nymphal skin abundances were: *amoena*: 20 and *sericans*: 12. A second smaller plot in the same ravine produced six nymphal skins of *sericans* and one *amoena*. The larger plot during the wet season (13 July 1974 census) produced two fresh skins of *F. mannifera* and one fresh skin of *Z. smaragdula*. Nymphal skins of *F. pronoe* and *F. spinocosta* were not searched for.

Discussion

Based on the limited data from this study, it is concluded that cicadas within the premontane-to-montane tropical moist forest zone in Costa Rica exhibit distinctive seasonal emergence patterns. Two seasonal adult emergence patterns are recognized based on my study: "dry season or tropical summer" cicadas, which include *F. semilata*, *F. "coffea"*, *F. amoena*, *F. pronoe*, *F. spinocosta*, *F. sericans*, and *Quesada gigas*, and "wet season or tropical winter" cicadas such as *F. mannifera*, *Z. smaragdula* and *Conibosa* sp. Therefore there is some evidence for allochronic annual emergence strategies in tropical cicadas within this major climatic and vegetation zone of Costa Rica, and presumably, to varying degrees, elsewhere in Central America. Extensive data on the geographical distribution of cicadas elsewhere in Central America are lacking. With the exceptions of *F. semilata* and *F. "coffea"*, all of the other cicadas studied have been observed to have the same seasonal adult emergence patterns in other major climatic and vegetation zones of Costa Rica (Young 1972, 1976, 1980a, b, 1981a; A. M. Young, unpublished data).

With the exceptions of but a few species, the genus *Fidicina* is predominantly associated with tropical dry seasons while *Zammara* with the wet seasons. *Fidicina* also represents the largest genus in Central America in terms of numbers of determined and partially-determined species, while *Zammara* is represented by two, possibly three, species based on current information. The monotypic genus *Quesada* is widely distributed in Central and South America, and also filters into the subtropical zone of North America, and it is a dry season form. Whereas the two species of *Zammara*

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Fig. 9. Collections of cicada nymphal skins over a two-year period from the three localities (lower and upper montane tropical moist forest) within the extensive coffee district northwest of the Meseta Centrale in Costa Rica. Data is for fresh skins only.

generally replace one another geographically in Costa Rica (A. M. Young, unpublished), there is considerable sympatry for the species of *Fidicina*. Because our knowledge of cicada natural history in the tropics is very meager, I hesitate to suggest that selection pressures such as competition have resulted in the evolutionary diversification and ecological differentiation of the genus *Fidicina*. Partial, tentative support of this view, however, is seen in the observed patterns of habitat partitioning in areas where several species occur together. An illustrative example would be the association of *F. pronoe* and *F. spinocosta* with secondary vegetation and the association of sympatric species such as *F. mannifera*, *F. amoena*, and *F. sericans* with primary forests. Such a pattern of ecological separation also occurs for these cicadas within the premontane tropical wet forest zone of Costa Rica (Young 1980b).

The proximal cues regulating the timing of annual emergences in tropical cicadas have not been determined and little is known about the adaptive significance of allochronic annual adult emergence patterns in these insects. Because many tropical habitats have assemblages of several species, allochrony may reduce competition for acoustical signal space, chorusing sites, and other space requirements related to reproduction. Patterns of habitat separation may be more related to resource requirements of nymphs.

Viewed within the context of ecological separation, examples of apparently microsympatric species of *Fidicina* such as *F. semilata* and *F. "coffeea"* beneath *Inga* trees in coffee plantations may have resulted from recent colonizations of these agricultural habitats when the original forest cover was cleared. Elsewhere (Young, unpublished manuscript) I have suggested that there is strong selection pressure favoring the exploitation of canopy-size Leguminosae trees in tropical forests because (a) various genera and species of Leguminosae are locally abundant in some forest habitats in different climatic and vegetational zones in Costa Rica (Holdridge et al. 1971) and elsewhere in the tropics, (b) the nymphal skins of many species of cicadas in tropical forests are very abundant beneath these trees (e.g., Young 1972, 1980a, b, 1981a; A. M. Young, unpublished) and abundances decline rapidly with increasing distance from these trees, and (c) the xylem fluids of root crowns of Leguminosae trees in tropical forests may have higher concentrations of nitrogen-containing nutrients such as amino acids than roots of other trees in the same habitats as a result of the nitrogen-fixing bacteria association with many legumes, thereby making these trees optimal feeding patches for developing cicadas. Cicada nymphs feed on xylem fluids (Cheung and Marshall 1973; White and Strehl 1978).

In a tropical region such as premontane-to-montane moist forest zone in Costa Rica northwest of the Meseta Centrale, one of the major coffee-growing districts of that country, intense removal of the forest cover and replacing it with a mosaic of coffee bushes and legume shade trees may have

allowed for the colonization of these areas by some species of cicadas already adapted for legume-feeding or to generalized legume associations in the original forest. From my observations of *Z. smaragdula* in this region and elsewhere in Costa Rica (Young 1980a; A. M. Young, unpublished), I predict that the apparent restriction of this cicada to *Zygia* trees along streams is due to sensitivity to low moisture availability in the soil rather than due to the kind of tree. Such an effect is particularly noticeable in my study from the observed distribution of *Z. smaragdula* nymphal skins near *Zygia* trees near water or low topographic points, while those of other legume-associated cicadas such as *F. semilata* and *F. "coffea"* are found with *Inga* trees on the upper slopes of coffee plantations. I doubt very much, if the legume-feeding hypothesis is correct, that *Zygia* root crowns are terribly different in terms of physical and nutritive properties from those of *Inga*, save for the difference in size (age) of the trees.

The observed densities of nymphal skins in coffee plantations for both *Fidicina* and *Zammara* falls well below densities for closely related species in relatively undisturbed forest habitats within the premontane tropical wet forest zone in Costa Rica (Young 1980b). The low densities are possibly due to the combined effects of (a) *Inga* trees, used as shade, being young or small relative to legume trees in natural forests, thereby providing less nutrients and other resources, (b) lower survival of cicada nymphs in the soil of coffee plantations and their very disturbed borders, and (c) low density courtship and oviposition by adult cicadas in the coffee plantation environment resulting from the even distribution of *Inga* trees over very large areas of the hills. Chorusing strategies in tropical cicadas are greatly influenced by the structure of the vegetation (Young 1980c, 1981b) which in turn may influence the oviposition behavior. If resources are abundant but rather uniformly distributed over large areas of habitat, the oviposition effort per resource patch may be low thereby generating low density distributions of developing cicadas.

Acknowledgments

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pleton, Wisconsin assisted with all aspects of the field work. Dr. Ridgway Satterthwaite, then Director of The Costa Rican Field Studies Program of The Associated Colleges of the Midwest (U.S.A.), assisted with field logistics. Voucher specimens of the cicadas studied are deposited in the permanent collections in the Section of Invertebrate Zoology at The Milwaukee Public Museum, and in The Museum of Zoology at The University of Michigan. I thank Karen Heerhold for typing the manuscript. This paper is dedicated to the kind folks of Grecia, Naranjo, and San Ramon who always remember fondly that big cicada of "Semana Santa," *Q. gigas*.

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Section of Invertebrate Zoology, Milwaukee Public Museum, Milwaukee, Wisconsin 53233.

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A LITTLE-KNOWN, ANONYMOUS WORK ON AMERICAN AND
EUROPEAN BUTTERFLIES AND MOTHS (1906),
WHICH SHOULD BE ATTRIBUTED TO WILLIAM
BEUTENMÜLLER (LEPIDOPTERA: NYMPHALIDAE)

Cyril F. dos Passos

Abstract.—This paper calls attention to an anonymous publication on butterflies and satisfactorily establishes the authors thereof.

It all began several years ago when my two friends, Mr. and Mrs. Allen L. Freas of Westfield, New Jersey, came to visit us and brought with them as a present to the author a small book on butterflies that they had found in their library and thought would be of interest. When it was noticed that this small book had been published under the auspices of the late William Beutenmüller, it occurred to the author to write to Miss Nina J. Root, Librarian of The American Museum of Natural History. She responded that, while the book was carded, it had disappeared from the shelves. Then commenced a search for another copy to replace it. One of the first responses was from a friend, Mr. William D. Field of the U.S. National Museum, who kindly loaned to the author his copy. But the greatest piece of luck was when in a conversation with Mr. Fred Lemmer, then president of the Newark Entomological Society, he disclosed that he himself had a copy actually given to him by Beutenmüller many years ago when Lemmer was a boy.

But let Mr. Lemmer tell his own story:

“Enclosed find the Beutenmüller Booklet.”

“About 47 years ago I used to accompany my Uncle Frederick Lemmer to the meetings of the Entomological Societies at the New York and Brooklin [*sic*] Museums and it was on these occasions that I met Mr. Beutenmüller and many of the other old time collectors.

“The little Booklet is a souvenir of one of those meetings.

“There is a possibility that Mrs. Beutenmüller made the pictures, as she was an artist and supposedly made all the pictures for the book of American Catocalas [*sic*].”

This work, entitled *A Manual of American and European Butterflies and Moths Reproduced in Natural Colors with Their Common and Scientific Names* to which is sometimes added, “prepared under the supervision of William Beutenmüller, Curator of the Department of Entomology, American Museum of Natural History, New York” was published about 1906 in at least two countries, the New York edition being by Funk and Wagnall’s

Company of New York and London. It was designed as a volume of the Standard Nature Series, and copies doubtless exist in many old-time private libraries.

Mr. Lemmer kindly gave his beautiful copy in original dust cover to the author, who in turn presented it to the Library of The American Museum of Natural History to replace the lost copy, where it is now kept in the Rare Book Room.

Mrs. Edna Hyatt Beutenmüller was an excellent artist, who assisted her husband in much of his work, and it is probable that she prepared the illustrations for the twenty-four plates of this manual, while her husband prepared the text explaining the figures, and one or both probably prepared the index. Mrs. Beutenmüller is described by Weiss (1943, p. 286) as an "entomological artist," and Barnes and McDunnough (1918) remarked:

"Ten plates of excellent water colors—drawings of the various species and two plates containing colored figures of the larvae, all drawn by the accomplished hand of Mrs. Beutenmüller."

This case is similar to that of the *Genera of Diurnal Lepidoptera* (1846–52), the title page of which lists the authors as Edward Doubleday and John O. Westwood followed by "Illustrated with eighty-six plates by William C. Hewitson." The latter phrase did not make Hewitson an author of the work or scientific names proposed in the work (see Hemming, 1941).

The work under consideration may be collated as follows: 1) dust cover with title, 2) title pages with different texts, only one seen with a year date (1860), 3) plates 1–24 with colored figures, 47 being butterflies and 67 moths, and 4) index, 3 pages with common names and references to plates and figures. The pages are about 14½ by 8½ mm.

No new names are introduced. Plate 13 figures the ova and larvae of the Chinese silkworm, *Bombyx mori*, natural size.

Acknowledgments

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Washington Corners, Mendham, NJ 07945.

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BOOK REVIEW

Butterflies and Moths of Newfoundland and Labrador: The Macrolepidoptera. Ray F. Morris. 1980. Publication 1691, Agriculture Canada. 407 pp., 34 color plates. Available for \$15 (Canada) or \$18 (outside Canada) from Canadian Government Publishing Centre, Supply and Services, Hull, P.Q. K1A 0S9, Canada.

This book represents an opulently produced documentation of a restricted, insular, boreal or near-boreal fauna, based on the published records of over a century and the author's personal collecting experience of some 25 years plus a large number of private and institutional collections. After a cursory survey of Lepidopterology in the region, its physical geography, and the seemingly obligatory material on basic biology, classification, and collection methodology, the book settles down to individual species accounts of all the butterflies and macro-moths. This is where the principal interest of the work lies, and this section deserves close scrutiny.

The book will be much sought-after for the color plates of moths, many of which have never been illustrated before—page after page of obscurely marked (and often obscure!) Noctuids and Geometrids in faithful color; this alone is worth the price of the book, and more. Unfortunately the butterfly plates are as consistently unpleasing to the eye as the moths are pleasing; a great many of the specimens are of inferior quality, and every imperfection is emphasized by the photographic technique—the pictures are back-lit. Several specimens are rubbed, a few are greasy, a number are poorly set, and the Pierids on plate 2 combine these flaws with poor color reproduction, the only such plate in the book. These problems will not bother the moth specialist. But both butterfly and moth collectors may be annoyed that no data are provided for the individual specimens illustrated, although there was plenty of room to do so; and the plate legends do not give page references to the text, forcing the reader constantly back to the index.

The species descriptions contain considerable new biological information, particularly on early stages, host plants, and distribution. Again, however, Morris' book resembles W. T. M. Forbes' *Macrolepidoptera of New York* in being fine for the moths but generally unsatisfactory for butterflies. For example, one of the strangest things in the Newfoundland literature is the assertion by Austin and Leila Clark (inexplicably, and repeatedly, spelled "Clarke" by Morris) in *Butterflies of Virginia* (1951) that the black form of the Tiger Swallowtail occurs there. One would think this book would either support or refute this claim; instead it merely quotes it (p. 36)—in the process listing both *P. glaucus glaucus* and *P. glaucus canadensis* as occurring on the island. This treatment of subspecies, like Austin Clark's own, betrays a fundamental misunderstanding of the subspecies concept, and it reappears

under *Nymphalis milberti*, where we learn that subspecies *milberti* and *viola* both occur on Newfoundland: "*milberti* is more prevalent in the north, whereas *viola* predominates in the south." And further, "the life-history of the two subspecies is probably very similar" (pp. 54-55).

Those whose interests are limited to diurnals will probably not want to buy this book, while moth collectors, especially in the Northeast and in eastern Canada, will find much of great value in it. Those who have published or are working up data for regional faunas may rightly turn green with envy over the plates.

Arthur M. Shapiro, *Department of Zoology, University of California, Davis.*

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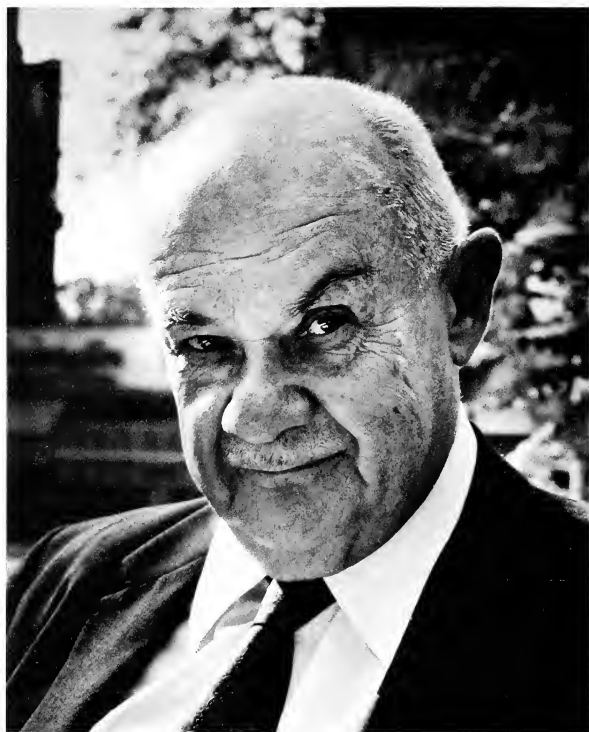
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DR. ROMAN VISHNIAC

Honorary Life Member, New York Entomological Society

Roman Vishniac was born in Pavlosk near St. Petersburg, Russia, on August 19, 1897. He received his M.D. and Ph.D. (biology) degrees in Moscow in 1920. Shortly afterwards, he fled to Berlin, where he conducted research in endocrinology, working at the same time as a photojournalist. From 1933 to 1939 he produced a photographic record of Jewish communities in Central and Western Europe and part of this unique work was published in 1947 under the title "Polish Jews." His activities attracted the attention of the Gestapo and during the Nazi regime he was imprisoned 11 times, kept twice in concentration camps, and forced to do hard labor. He was sentenced to death twice but fortunately managed to escape and emigrated to the United States in 1940. In New York he became a research associate in anatomy at Albert Einstein College of Medicine and, in 1961, professor in the Department of Biology Education at Yeshiva University. At the same time he also served as project director and film maker for the Living Biology film series of the National Science Foundation, applying his pioneering time-lapse cinematography and light-interruption techniques as

well as color photomicroscopy of living organisms to produce a classic and fascinating film series. His chief biological researches, in addition to entomology, have been in protozoology, marine microbiology, physiology of ciliates and circulation systems in unicellular plants. He originated the hypothesis of the polyphyletic origin of life, according to which the first living organisms were multicellular structures that emerged many times in many places by different biochemical pathways. In 1971 a volume of his splendid color micrographs of proteins, vitamins, and hormones, entitled "Building Blocks of Life" was published.

Dr. Vishniac is fluent in most European and several Asian languages. He is an expert in Far Eastern art and philosophy, and a recognized art historian and science historian as well as a bibliographer. He has one of the largest collections of science books, including many old and very rare volumes. He has taught, among others, at City University of New York and Case Western Reserve University and he is Chevron Professor of Creativity, teaching at present at the Pratt Institute in Brooklyn and in Manhattan.

Dr. Vishniac served for two years as President of the New York Entomological Society. Among his many honors and awards was the Eastman Kodak Gold Medal, which he received "in recognition of outstanding contributions which lead to new and unique educational programs, utilizing motion pictures and instrumentation photography." At present, Dr. Vishniac is working on a new book, entitled "The World that Disappeared."

Karl Maramorosch

PREPUPATION BEHAVIOR AND PUPATION OF THE
PREDACEOUS DIVING BEETLE *DYTISCUS VERTICALIS*
SAY (COLEOPTERA: DYTISCIDAE)

Daniel R. Formanowicz Jr. and Edmund D. Brodie Jr.

Abstract.—Preceding pupation, *Dytiscus verticalis* larvae burrow into soil above the waterline. They construct pupal cells using mandibles, legs, and body wriggling. Pupal cells are nearly spherical and the openings are sealed from the inside with soil placed there by mandibles. Beetles spent 20 to 34 days in pupal cells. Newly eclosed adults are white but darken in 8 to 14 h. Pupae are described.

Introduction

Information concerning prepupation behavior and pupal stages of North American Dytiscidae is either lacking or fragmentary. In his review of dytiscid biology, Bertrand (1972) presented descriptions of larvae and pupae of some species. Matheson (1914), Wilson (1923), and Leech and Chandler (1956) have presented accounts of dytiscids which form pupal cells by burrowing into mud. James (1969) described eggs, larvae, and pupae of five species of dytiscids, all of which apparently construct pupal cells in mud along pond margins. However, actual construction of a pupal cell was only observed for one species, *Acilius semisulcatus* Aube (James 1969).

Dytiscus verticalis occur in shallow, weedy, temporary and permanent ponds in woodlands and open fields. The larva was described by Wilson (1923) but the pupa is undescribed.

This paper describes pupal cell construction behavior, pupal cells, pupal stages, length of pupation, and length of time to full coloration for *Dytiscus verticalis* reared under laboratory conditions.

Methods

Two hundred and fifty-six *D. verticalis* larvae were collected from four ponds on or near the E. N. Huyck Preserve, Rensselaerville, N.Y.; 50 of these were used in the lab rearing study. Observations from two pupae found along margins of two of these ponds are also included. Larvae were held in circular plastic chambers 15 cm in diameter, 6.5 cm in depth, and contained 4 to 5 cm of water. Each larva was fed several frog tadpoles (*Rana*, *Hyla*) and/or salamander larvae (*Ambystoma*) daily.

Beetle larvae which appeared ready to pupate (ceased feeding, became lethargic, and did not strike at prey) were measured by displacement volume

(this method was used to minimize the risk of injury during handling, Brodie et al. 1978) and transferred into water of one of the three types of chambers described below.

(a) *10 gal. glass aquaria (26 × 51 cm).*—These chambers had a maximum soil depth of 15–20 cm, a soil slope 30 cm long (approx. 30°), and water added at one end to a depth of 3 to 4 cm.

(b) *20 gal. glass aquaria (30 × 76 cm).*—The slope was 60 cm long (approx. 20°), maximum soil depth was 11 cm, and water depth was 5 cm.

(c) *Circular plastic chambers (15 cm diameter).*—These chambers contained no standing water but had a level layer of moist soil 4.5 cm deep.

Behavior of each larva was observed continuously for two hours after introduction into one of the chambers. For descriptive purposes representative pupae were uncovered and preserved at 7 and 14 days (4 and 1 respectively) after the larval skin was shed. Length of pupation and time from eclosion to attainment of adult coloration were recorded. Dimensions of some pupal cells were measured after the adult had left or was removed. Pupal cells of two field collected pupae were also measured and the pupae immediately preserved. Newly eclosed and fully colored beetles were sexed and preserved.

Results

A) *Pupal cell construction.*—Five categories of behavior were sequentially involved in the construction of a pupal cell after the beetle crawled onto the soil. 1) The initial hole was dug by moving mud pellets with scooping motions of the legs and pushing motions of the head (observed in 21 larvae). This hole was usually as wide as the larva and at least one-half its length deep. 2) Eleven larvae were observed to push their bodies head first into this initial hole which they widened and deepened by body wriggling. 3) During the widening process described above, 12 beetle larvae were observed to move pellets of mud out of the hole by grasping them with their mandibles. 4) Mud pellet grasping was used by 12 larvae to form the pupal cell into a roughly spherical shape. 5) Finally, 12 larvae closed the cell from the inside by placing pieces of mud in the hole with the mandibles.

Pupal cell construction was completed in 20 min to 12 h. Variability in amount of time needed to complete a pupal cell may have been the result of differences in soil texture or moistness within the chambers. The size of the *Dytiscus* larvae placed into chambers to pupate varied from 1.4 to 2.0 cc (\bar{x} = 1.79 cc).

Mean vertical diameter of pupal cells in the lab was 35 mm and mean horizontal diameter 36 mm. Pupal cells found in the field were 26 × 35 mm and 28 × 32 mm. Cells in chambers a and b were located from 220 to 590 mm (\bar{x} = 338 mm) upslope from the water at soil depths of 64 to 110 mm

Table 1. Description of 5 pupae, 7 (a, b, c, d) and 14 (e) days after shed of the larval skin.

	Pupa				
	a	b	c	d	e
Total length (mm)	31	35	36	37	36
Max. width (mm)	12	15	9	13	16
Setae number					
Head	60	47	53	43	62
Pronotum	148	134	144	131	141
Mesonotum	9-M-9	9-M-7	7-M-6	6-M-6	8-M-7
Metanotum	6-M-6	5-M-6	6-M-5	7-M-6	6-M-7
Abdominal segments					
1	7-M-7	6-M-8	7-M-7	5-M-6	6-M-6
2	9-M-10	10-M-9	9-M-10	8-M-7	7-M-6
3	10-M-8	10-M-6	9-M-8	6-M-8	8-M-7
4	8-M-9	9-M-6	9-M-9	7-M-8	10-M-9
5	8-M-7	9-M-9	8-M-9	6-M-6	8-M-9
6	8-M-8	9-M-7	8-M-8	6-M-5	9-M-8
7	17-M-18	20-M-14	16-M-13	17-M-14	19-M-12
8	26-M-26	29-M-25	27-M-33	27-M-24	25-M-30
Sex	♂	♀	♀	♂	♀

(\bar{x} = 89 mm). The floor of three pupal cells was below the waterline and one of these three pupae successfully eclosed. There were 44% males and 56% females among the successfully reared beetles. There were no consistent differences between the three types of chambers in the parameters that were measured.

B) Description of pupa.—The following description is based on the combined observations on two male and two female 7-day pupae and one female 14-day pupa (Table 1).

Measurements of lab reared pupae: length—31 to 37 mm (\bar{x} = 34.8 mm); maximum width—9 to 16 mm (\bar{x} = 12.3 mm). Measurements of field collected pupae: length—32 to 36 mm; maximum widths—11 to 14 mm. Caudal cerci 2 mm long in all pupae.

Head setae arranged as follows (\bar{x} = 50.8): 14 to 18 along continuous anterior curve between eyes; 1 to 3 at inner posterior corner of each eye; 2 to 3 in each of two groups ventromedial to each eye; and 21 to 32 across posterior margin of head.

Pronotum with 131 to 148 setae along the lateral, posterolateral, and anterior margins and along disc. Setae on mesonotum, metanotum, and eight abdominal segments variable and unequal on opposite halves of pupae (see Table 1) (formula used to indicate number of setae on left and right halves of each pupa is from Spangler (1973), midline is indicated by—M—between



Fig. 1. Newly eclosed adult *Dytiscus verticalis* in pupal cell.

the numbers). Ninth abdominal segment terminates in two cylindrical cerci, each bearing 40 to 50 setae. One pair of spiracles on first six abdominal segments, located on each anterolateral corner.

Antennae directed ventrally underneath head, between the wing pads and the femora. Tibiae of first two pair of legs folded against femora with tarsi

parallel to body axis. Metafemur and metatibia under hind wing pads and not folded; metafemora are directed away from the tibia toward the midline.

Dorsal setae associated with thick spine-like projections which are largest along midline of fifth abdominal segment.

C) *Coloration*.—Immediately after shedding larval skin (7 days after cell construction), pupa was white but changed to yellowish-white within a few hours. Legs, antennae, and mouth parts darken 7 days after eclosion. Pupae light brown with dark brown appendages just prior to eclosion. Length of time in pupal cell varied from 20 to 34 days (\bar{x} = 24.9 days).

Newly emerged adults were white (Fig. 1). Wing covers expanded to cover the abdomen within five minutes of eclosion and were white with longitudinal brown streaks. Eyes and tip of abdomen were dark brown. Adult pigmentation developed dorsally and ventrally from posterior to anterior in a V-shaped pattern and took from 8 to 14 h (\bar{x} = 10.5 h). Beetles remained in pupal cells throughout this process. Subsequent period of time spent in pupal cells was not determined. Fully colored adults were transferred to circular plastic chambers (half filled with water and half with soil). All newly eclosed adults fed within 24 h of eclosion (0.2 cc *Hyla* tadpoles).

Discussion

Dytiscus verticalis has a larger pupal cell and a longer pupation period than either *D. fasciventris* Say or *Acilius semisulcatus* which James (1969) described. This is probably because *D. verticalis* is larger in all life stages than either *A. semisulcatus* or *D. fasciventris*. *Acilius semisulcatus* also exhibits at least one of the categories of pupal cell construction behavior that we observed in *D. verticalis*. James (1969) described soil grasping using the mandibles by *A. semisulcatus* during pupal cell construction.

There was no apparent difference in pupal cells between lab reared and field collected *D. verticalis* pupae. However, eclosion success of beetle larvae which had constructed cells in the lab (50%) may have been different than under field conditions. Other factors such as drying and predation (one field collected pupae found by us had been killed by ants) may lower eclosion success in natural situations.

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(DRF) Biology Department, State University of New York at Albany, Albany, New York 12222 and (EDB) Biology Department, Adelphi University, Garden City, New York 11530.

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INSECT SUCCESSION IN THE DECOMPOSITION OF A MAMMAL IN COSTA RICA¹

Luis Fernando Jirón² and Víctor M. Cartín²

Abstract.—Observations were made on the decomposition of a dead dog during the dry season of 1977 in the Central Valley of Costa Rica, Central America. The terrain is classified as premontane humid forest and the observations were made in a secondary forest. The general pattern of decomposition was basically the same as has been described by authors in other latitudes, but different in the ecological complexity and the insect fauna involved. The classification used for human cadavers by forensic pathologists in Costa Rica and other countries in the American tropics was utilized in this study. It includes the following stages: discoloration, emphysematic (bloated), liquefaction and skeletal remains. The succession of different species appeared to depend on their specific feeding preferences, interspecific competition, and the microclimate provided by the substratum. Marked changes in the activity of populations during crepuscular periods coincided with an increase in relative humidity and a decline in temperature in the macroenvironment of the surrounding forest. Included among the principal insect consumers of the remains were the calliphorid dipterans *Phaenicia eximia* Wiedemann and *Hemilucilia segmentaria* Fabricius, the piophilid dipteran *Prochyliza azteca* McAlpine and the coleopteran *Dermestes carnivor* Fabricius. The most important predators were the histerids *Euspilotus aenicollis* Marshall, *Hister punctiger* Paykal and *Geomysaprinus* (*Priscosaprinus*) *beliocolus* Marshall. Some of these species have also been associated with a similar type of substratum in the tropical rain forest and tropical dry forest in Costa Rica.

Introduction

Much is known about the behavior and taxonomy of the principal groups of insects that participate in the successional stages of decomposition in temperate zones, but relatively few studies have been made in tropical zones (Bohart and Gressitt 1951; Cornaby 1974; Payne 1965). Previous studies have shown that certain general patterns exist during the decomposition process that accounts for the natural or slightly altered ecological conditions. The decomposition phenomenon, although it presents a continuum of changes, has been divided into various phases or stages in order to facilitate its study

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² Temporary address: Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706, U.S.A.

(Johnson 1975; Payne 1965; Reed 1958). Given the limited knowledge of this process in the neotropical region, the objective of our study was to interpret and characterize the decomposition process in a dead dog, and to determine the principal insect species that were present.

Materials and Methods

Field observations were made during the dry season of 1977 in a secondary forest on the campus of the University of Costa Rica, in San José, Costa Rica, Central America. The altitude of the study area is 1,200 m. The substrate utilized was a dead female dog that had been euthanized with nembutal (Pentobarbital). The carcass was placed on the floor of the forest and observations were made each day for 28 days, every four hours from 0600 hours to 1800 hours with an additional observation at 2000 hours. From the 28th through 48th day, observations were made every 4th day, and subsequent observations were made on days 58, 70, 80 and 90. At each observation period, recordings on temperature, relative humidity, state of decomposition of the dog, dominant insect population and predation were made. Samples of adult and larval insects were collected for later identification. Larvae were reared to the adult stage for identification. Particular attention was given to the collection of the most abundant species. Rarer species were grouped according to the similarity of their ecological function and identified only to family level.

Results and Discussion

Our observations indicated that decomposition in the tropics has the same general pattern as described for temperate zones. The differences are principally in the number and duration of the phases, the insect faunae involved and the degree of ecological complexity (Johnson 1975; Payne 1965; Reed 1958). In our study we utilized the classification used by forensic pathologists in Costa Rica and other Latin American countries for human cadavers (López and Gisbert 1962; Vargas 1977). This classification divides the decomposition process into four phases as follows:

Discoloration.—Color changes begin immediately following death and include pallid color of the lips, nose, feet and abdominal region and green color of superficial veins. Hobson (1932) found that during this initial period the tissues are acid and not suitable for feeding by fly larvae, which feed on the liquid between muscle fibers. Later, the tissues become alkaline, the sarcolemma dissolves and the intermuscular tissue is attacked by the larvae. In our study this phase lasted approximately three days (Fig. 1). During this period we observed the presence of ants (*Camponotus* sp.), muscoid, sarcophagid and drosophilid flies and a large number of the calliphorid, *Phaenicia eximia* Wiedemann, which oviposited in the throat region near the nasal fossae, and in the eyes, mouth, vagina and anus.

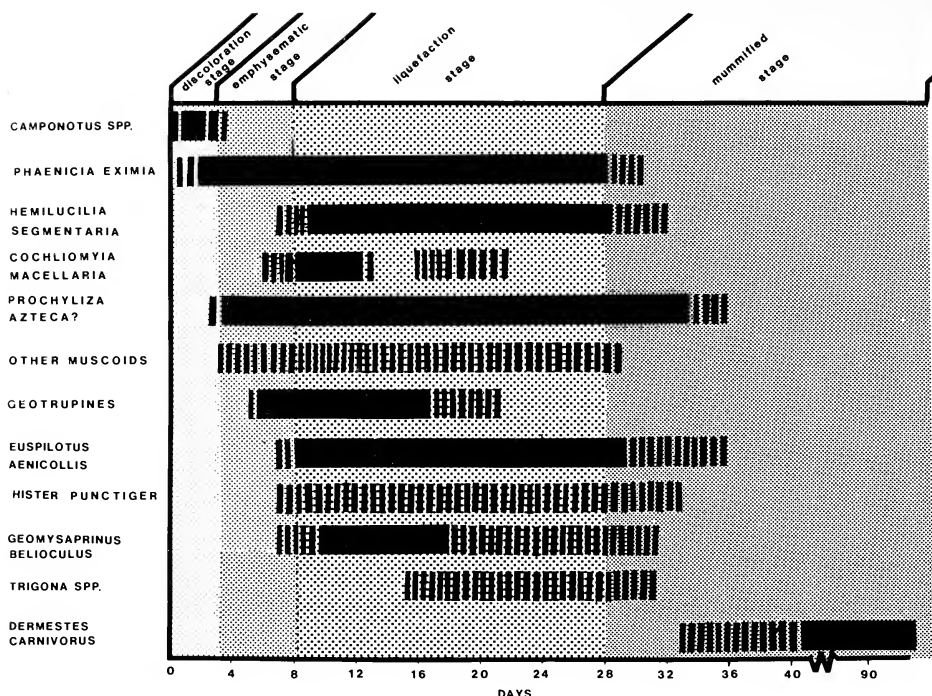


Fig. 1. Appearance of insect populations thru the necrologic stages of decomposition of a dead dog in the Central Valley of Costa Rica, during dry season of 1977. ■ High population density, |||| low population density.

Emphysematic state.—This state of degradation is characterized by marked tumefaction of the abdomen and other body regions and protrusion of the eyes and tongue. This condition is caused by anaerobic decomposition of the proteins and is subject to individual variation (Johnson 1975; Payne 1965; Reed 1958). Duration of this period is variable and probably depends on the temperature and other environmental conditions.

In this study, this phase lasted approximately four days. During this time the main insects observed were large foci of active larvae in the anal and mandibular regions. The majority of the specimens collected from these two regions were *P. eximia*. At night, adults of the histerid beetle *Euspilotus aenicollis* Marshall, and certain geotrupine scarabs comprised the majority of the active faunae. This group of Coleoptera hid during daylight hours in holes dug into the soil near or beneath the body of the animal. Similar behavior was also observed by Payne (1965) in the temperate zone. During the final part of this phase, bare areas developed near the soil interphase due to hair slippage. Several muscoid flies were observed ovipositing on these fleshy exposed regions.

Liquefactive stage.—This stage is characterized by the liquefaction of the

viscera and soft tissues. It begins with breakage of the skin in one or more places, permitting entry of air and leading to aerobic decomposition (Reed 1958). Johnson (1975) interpreted this phase as a general deterioration of the tissues until only dried tissues and bones remained, with a loss of 90 percent of the original weight of the carcass. This degenerative phase corresponded to what Payne (1965) divided into two steps: active decay stage and advanced decay stage.

In the present study, this phase began on the 8th day and lasted approximately 19 days. During this phase we observed the greatest activity by necrophilic insects, both in the size of population present and the variety of species.

In the initial part of this phase we observed that the remains of the animal underwent rapid deterioration. Muscoid fly larvae of various species, in various stages of development, constituted the most conspicuous group of insects, but the majority of the pupae collected were of *P. eximia*, the pioneer species. It is important to note that this calliphorid completed two or perhaps three generations during degradation of the carcass, and, together with *Hemilucilia segmentaria* Fabricius and the piophilid *Prochyliza azteca* McAlpine were the most abundant species during this phase of decomposition. Adult insects, including silphids and other Coleoptera were observed but not identified to species level.

The abundance of fly eggs and larvae attracted numerous predators. These were most abundant at night and included staphylinids, and especially histerids (*E. aenicollis*, *Hister punctiger* Paykal, and *Geomysaprinus* (*Priscosaprinus*) *beliocus* Marshall). Other species occasionally observed included dermapterans, an ichneumonid, some forest roaches, wasps (probably of the genus *Stelopolybia*), bees of the genus *Trigona* and lepidopterans (Pyralidae and Noctuidae), none of which were identified to species.

After twelve days there was a marked decline in the population of adult muscoids visiting the carcass, although larval activity was still very intense. We observed an increase in the quantity of pupae in the soil around the remains of the animal. A new focus of larval activity occurred in the thoracic region, which included larvae of *P. eximia*, *H. segmentaria* and *Cochliomyia macellaria* Fabricius. At night, histerids and certain staphylinids were the most abundant predators.

After twenty days, the remains of the dog were dehydrated and the dynamics of the decomposition process began to slow. Activity of the larvae of the necrophilic species was reduced and they began to migrate to the

³ On the 18th day we observed a recent human fecal deposit 15 meters from our study material. Insects attracted to the feces included adult sarcophagid, muscid and calliphorid flies with *C. macellaria* and *P. eximia* the most abundant species, although as noted above, they were absent as adults on the remains of the dog at this time.

lower and internal areas where moisture content was higher. Emergence of adult forms, which began on the 18th day became more marked. Histerids, staphylinids and some dermestids (this latter group had recently appeared) were active in the same areas in which fly larvae were found.

During the following days the process of dessication became more accentuated and larvae of calliphorids and other groups were restricted to small more liquid zones. Recently emerged adults left the area. Numbers of *P. azteca* and other small dipterans that had been constantly present during most of the degradation process also diminished considerably. Populations of predators during the final part of the liquefactive phase were eventually limited to the histerids, *E. aenicollis*, *H. punctiger* and *G. belioculus*. Visits by bees of the genus *Trigona* became most frequent as they collected material for construction of their nests (Wille 1965).

Mummification.—The process of decomposition was virtually interrupted in the liquefactive phase. Instead of continuing to a state termed "skeletal remains" by forensic pathologists, however, a process of mummification began. This phenomenon occurs frequently in tropical zones under conditions of low humidity, high temperature and appropriate air circulation (Vargas 1977).

During our study period (1–28 February 1977) there was no rain, and warm air circulated over vegetational cover of the forest, contributing to a high degree of mummification of the remains. A large proportion of the muscle tissue dried and became hard, principally those areas in direct contact with the sun's rays. However, it was possible to observe a few larvae and pupae of muscoid flies in these lower zones that were in contact with the soil.

On the thirty-second day we began to observe the presence of adult dermestids (which had disappeared many days before) and on the fortieth day there appeared the first larvae of *Dermestes carnivorus* Fabricius, which later increased to high population levels. These larvae constituted the dominant population at least until approximately day ninety. The remains were consumed by the larvae of this coleopteran through the skeletal phase at the end of the dry season, when our observations ceased.

Temperature and humidity.—The effects of temperature and humidity on the behavior of populations of necrophilic insects have been observed by various authors. Reed (1958) did not note appreciable changes in the activity of necrophilic insects during periods of rainfall, while Payne (1965) stated that the activities of insects involved in the putrefactive process were influenced more by temperature than by other environmental factors.

We observed a marked change in the activity of larvae and adults at the beginning and end of daylight period. During our initial 28 day observation period, diurnal temperature was relatively constant, ranging from 18.5°C to 20°C between 0600 hours and 2000 hours. During the night, relative humidity was usually 100% and temperature about 15°C.

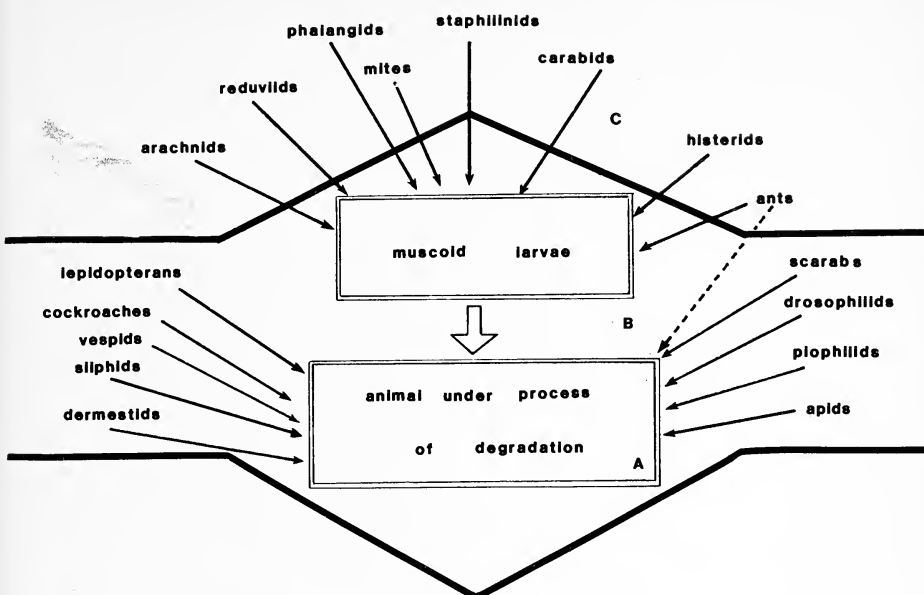


Fig. 2. Trophic relationships observed among arthropods associated with the carcass of a mammal in a premontane humid forest. Trophic levels: A. animal under process of degradation, B. Primary consumers, and C. Predatory insects.

During the dry season temperature and humidity are relatively stable during daylight hours. However, atmospheric conditions are less stable during the rainy season in the Central Valley of Costa Rica. During the months of October and November of 1974 (rainy season) one of us (L. F. J.), working in a preliminary study in the same forest, observed a clear reduction in the activity of adult and larval muscoid flies associated with a dead armadillo (*Dasypus novemcinctus*) on cold cloudy days.

Feeding relationships.—Trophic levels associated with the decomposition of the vertebrate comprised three categories (Fig. 2). The first level was comprised of the material undergoing degradation by bacteria and fungi. The second level was comprised of primary consumers including larval and adult coleopterans, principally of the families Silphidae, Scarabaeidae and Dermestidae and dipterans of the families Calliphoridae, Drosophilidae, Chloropidae, Otitidae, Piophilidae, Phoridae and Sarcophagidae. Other primary consumers included certain Hymenoptera, Lepidoptera and roaches that occasionally fed or extracted material from the substrate. The third level was comprised of secondary consumers that were predators of the primary consumers. These predators were principally histerids, staphylinids, vespids, ants, phalangids, chilopods and reduviids. In the primary study mentioned above, during the rainy season we observed a greater variety of

secondary consumers which included practically the same groups as seen during the dry season plus other arthropods: carabids, spiders, abundant mites *Macrocheles muscadomesticae* (Scopoli) and a braconid mycrohy-menopteran which was a parasite of fly pupae.

Appreciable differences in the time of appearance of the different necrophilic species were observed during the process of decomposition (Fig. 1). The presence and abundance of a given species appeared to depend largely on its microclimatic and feeding tolerances and preferences. There was not a strict relationship between a given decompositional stage and the presence of any particular species. For example, the piophilid *P. azteca* was present for many days, independent of the stage of decomposition, probably because this insect feeds on secretions and exudations of the carcass, and its environmental and feeding preferences are apparently wide. The presence and abundance of larval and adult stages of a given insect varied. For example, the calliphorid *P. eximia* was present for a long period of time, although the adults were not attracted to the carcass after the second half of the liquefactive phase. However, they and other muscoid flies were present in the area as was evidenced by attraction to fresh human feces in the vicinity.

Temperate zone studies have shown seasonal variation in the occurrence of muscoid species in carcass substrates (Johnson 1975; Reed 1958). Denno and Cothran (1975) indicated that in addition to seasonal variations, the size of the carcass and intraspecific competition among the necrophilic insects influence the presence of fly species. We found that some calliphorid species occur throughout the year in the tropics, although there may be variations in population densities related to season of the year and the types of substrates available (Cornaby 1974; Jirón 1979).

The presence of *Dermestes carnivorus* also appears to depend on the biochemical condition of the carcass and on the microclimate. Favorable conditions for development of large dermestid populations were present after the cessation of the liquefactive phase, when large portions of the carcass began to dry. The absence of rain also appears to favor the presence of this coleopteran, which was present for several weeks in the dried carcass. This requirement for dry conditions may explain the fact that dermestids appear sporadically during the liquefactive phase and later disappear, before reappearing in the mummification stage.

The presence of the predators *H. punctiger*, *E. aenicollis*, *G. belioculus* and others depends mainly upon the abundance of fly larvae, microclimatic conditions, and probably interspecific competition. State of decomposition in the carcass did not affect these predatory insects directly. It is important to note that several of the principal species observed in our study in the Central Valley of Costa Rica (premontane humid forest) were observed also by Cornaby (1974) in tropical humid and tropical dry forest of the same country. Also the calliphorids *P. eximia*, *H. segmentaria* and *C. macellaria*

have been found associated with human cadavers in the liquefactive stage in several regions of Costa Rica (Jirón 1979).

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(LFFJ) Departamento de Parasitología, Universidad de Costa Rica, San José, Costa Rica, C.A. and (VMC) Escuela de Ciencias Agrarias, Universidad Nacional, Heredia, Costa Rica, C.A.

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COMPARISON OF TWO SAMPLING METHODS FOR
*LEPTOTHRIPS MALI*¹ IN VIRGINIA
APPLE ORCHARDS

M. P. Parrella,² J. P. McCaffrey and R. L. Horsburgh

Abstract.—A destructive and time-consuming limb-tap sampling method was demonstrated to be 88% efficient for capturing adult and 2nd larval stage *Leptothrips mali*. This sampling method was compared to a simple, non-destructive, but inefficient, visual sampling technique through regression analysis. A significant relationship was found which indicated that the visual technique may be a practical sampling method.

Predaceous thrips have been sampled from deciduous fruit trees by tapping limbs over a cloth covered tray (Putnam 1965; Parent 1967; Horsburgh and Asquith 1968; Holdsworth 1968) and by visual examination of the foliage for timed periods (Clancy and Pollard 1952). Problems associated with the limb-tap method are the amount of time required, damaged limbs and dislodged fruit. Visual searching of the foliage for *Leptothrips mali* (Fitch) is practical because the adults are black and 2nd larval stages are reddish-brown which allows these stages to be observed against the green foliage. Unfortunately, this technique greatly underestimates the thrips' population on the tree because these predators are not always on the leaves where they can be observed.

To circumvent these problems, the efficiency of the limb-tap technique for capturing thrips was evaluated and regression analysis was employed to determine the relationship between thrips' numbers obtained utilizing a visual search and the limb-tap technique.

Materials and Methods

The efficiency of the limb-tap technique for sampling adult and 2nd larval stage *L. mali* was evaluated in 1977. An abandoned orchard which had not been sprayed for ca. 10 years was used as the study area. Several cultivars were present in the 3.2 ha orchard but Golden Delicious was the only cultivar sampled; trees were 15 years old and ca. 4 m in height. Eight trees were arbitrarily chosen within the orchard and three limbs (ca. 3.2 m high) were selected from the northern, western and southeastern sectors of each

¹ Thysanoptera: Phlaeothripidae.

² Present address: Dept. of Entomology, University of California, Riverside, CA 92521.

Table 1. Efficiency of the limb-tap method for dislodging *Leptothrips mali*.

Tree no.*	Mean numbers of <i>L. mali</i> **						Percent capture***		
	Dislodged			Remaining					
	19-V	2-VI	21-VI	19-V	2-VI	21-V	19-V	2-VI	21-V
1	22	32	28	2	7	3	91.6	82.0	90.3
2	25	36	37	2	6	1	92.6	85.7	97.4
3	9	57	71	1	10	2	90.0	85.0	97.3
4	14	31	49	0	7	2	100.0	81.6	96.1
5	3	42	27	0	8	4	100.0	84.0	87.1
6	2	48	15	0	6	3	100.0	88.9	83.3
7	14	32	5	2	3	0	87.5	91.4	100.0
8	8	21	24	0	1	4	100.0	95.5	85.7

* 3 limbs per tree were tapped for thrips and subsequently examined in the lab for remaining thrips.

** Means from 3 limbs per tree.

*** No. dislodged ÷ no. dislodged + no. remaining.

tree. The outer meter of each limb was tapped (five taps per limb) with a rubber-coated stick over a 1 m² muslin cloth-covered tray. The tray was searched for about 15 min. and the number of thrips dislodged per limb was counted. Immediately after tapping, each limb was covered with a polyethylene bag, clipped, and taken to the laboratory. The limb and bag were carefully examined for remaining thrips within 48 h. Sampling was on three dates; separate trees were sampled only once.

In 1978 this study area was used to determine the relationship between the numbers of thrips counted while visually searching the foliage and the numbers obtained when the same foliage was tapped. Thrips were counted visually on Golden Delicious trees while walking around one-half of a tree for 3 min. The natural position of any part of the tree was not disturbed during the inspection. The visually searched area was then tapped with a rubber-coated stick over a 1 m² muslin cloth-covered tray. *L. mali* falling on the tray were collected and counted. Sampling was on five dates at 2-week intervals beginning in mid-June. On each sampling date six trees were arbitrarily chosen in the orchard; separate trees were sampled only once.

Regression analysis was calculated using the General Linear Model procedure (Barr et al. 1976) with the limb-tap and visual data as independent and dependent variables, respectively.

Results

The efficiency of the limb-tap technique for capturing adult and 2nd larval stage *L. mali* ranged from 82 to 100% ($\bar{x} \pm \text{S.D.} = 88.7 \pm 14.6$) (Table 1). The relationship between the mean numbers of *L. mali* obtained in a visual

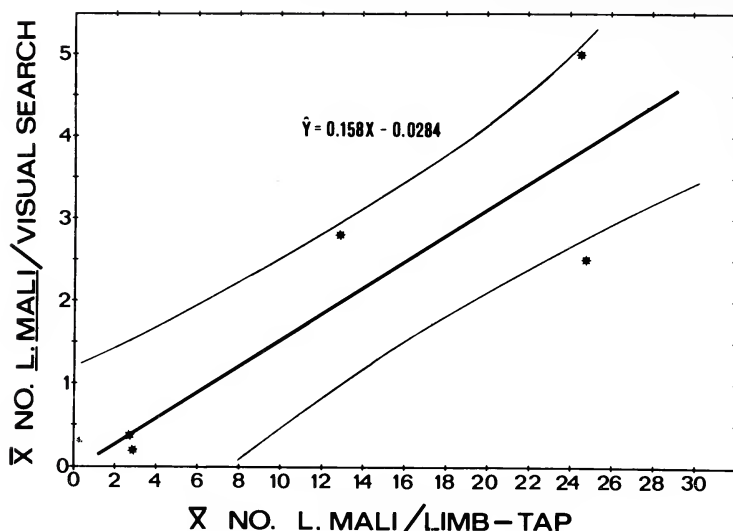


Fig. 1. Relationship between the number of *L. mali* observed and limb-tapped from 6 Golden Delicious trees on 5 sampling dates, 1978 ($R^2 = 0.76$). 95% confidence bands are included.

search and limb-tap is presented in Fig. 1. A significant ($P < 0.05$) R^2 value of 0.76 (based on 5 sampling dates) was obtained indicating that 76% of the variation in the numbers of *L. mali* obtained in the visual search is explained by their linear relationship with the limb-tapped numbers of thrips.

Many factors can affect this relationship including observer efficiency, tree height, cultivar, density of *L. mali* and its prey (mites), environmental conditions, etc. These would have to be taken into consideration and evaluated before the relationship between the limb-tap and visual search can be employed in a sampling program. The visual search is 6 times faster than the limb-tap (3 min. vs 15–20 min.) and may be of use in a study of population dynamics where an arbitrary rather than an optimum sampling plan is acceptable (Morris 1960).

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Department of Entomology, Shenandoah Valley Research Station, Virginia Polytechnic Institute and State University, Steeles Tavern, Virginia 24476.

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THE EUROPEAN KATYDID *MECONEMA THALASSINUM*
(DEGEER): NEW LOCALITY RECORDS FOR
NORTH AMERICA (ORTHOPTERA: TETTIGONIIDAE)

E. Richard Hoebeke

Abstract.—*Meconema thalassinum* (DeGeer) is recorded from Rhode Island and New York. These records represent new United States localities for this European katydid which was first detected in North America in 1957 on Long Island, New York.

The presence of the European katydid, *Meconema thalassinum* (DeGeer), in eastern North America was first reported by Gurney (1960, 1960a). The first specimens (two males and two females) were collected in July and August 1957, and again in July 1959 (one male and one female) at Little Neck, Long Island (Queens County), New York. Johnstone (1970) reported the second collection of this species with the capture of a single male specimen in August 1968 at King's Park, Long Island (Suffolk County). A third collection of five specimens (three males and two females) at Scarsdale and Larchmont (Westchester County), New York during July and August from 1974-77 was made by Sismondo (1978); he also observed that the nest provisions of *Sphex ichneumoneus* (Linnaeus) (Hymenoptera: Sphecidae) were comprised exclusively of *Meconema thalassinum*. A fourth collection of thirteen specimens (ten males and three females) at Garden City, Long Island (Nassau County) in July 1977 was documented by Smith (1979). It is my purpose in this note to provide two new additional records for *M. thalassinum* which extend the known distribution of this introduced species in North America (Fig. 1).

As a result of the USDA-APHIS "High Hazard Pest Survey" program, a single female specimen of *M. thalassinum* was recently submitted to me for identification; this specimen was collected in a nursery at Middletown, Rhode Island (Newport County) on 14 August 1980 by R. B. LaFrance.

In addition, a thorough search of the undetermined Tettigoniidae in the Cornell University Insect Collection (Ithaca, New York) uncovered another new record; one male specimen was collected on the campus of Cornell University (Comstock Hall) in July 1974 by J. A. Schafrik.

Both specimens are deposited in the Cornell University collection.

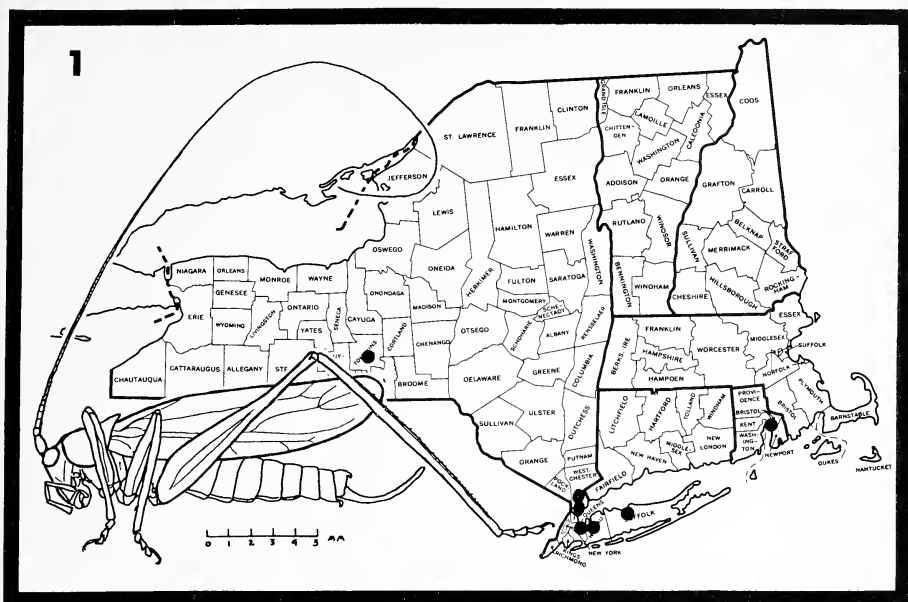


Fig. 1. Known distribution of *Meconema thalassinum* (DeGeer) in eastern North America (male habitus drawing adapted from Smith, 1979).

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Department of Entomology, Cornell University, Ithaca, New York 14853.

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SYNONYMY AND DISTRIBUTION RECORDS IN THE GENUS
EUCERCERIS (HYMENOPTERA: PHILANTHIDAE)¹

George R. Ferguson

Abstract.—*Eucerceris ferruginosa* Scullen is removed from synonymy with *E. nevadensis* (Dalla Torre). *E. baja* Scullen is the male and a junior synonym of *E. ferruginosa*. *E. nevadensis mojaviensis* Scullen (New Status) is the correct name for the taxon north of Mexico previously referred by authors to *E. nevadensis ferruginosa* nec Scullen. The following synonymy is presented: *E. lacunosa* Scullen (= *E. lacunosa sabinasae* Scullen, New synonym); *E. morula* Scullen (= *E. morula albarenae* Scullen, New synonym); *E. superba* Cresson (= *E. bicolor* Cresson, = *Cerceris dichroa* Dalla Torre, New synonyms); *E. canaliculata* (Say) (= *E. zimapanensis* Scullen, New synonym). The male of *E. lapazensis* Scullen is characterized, and the distribution of several species is discussed.

Eucerceris is a North American genus distributed as far south as Panama. A transverse depression on each of the middle gastral terga separates it from the closely related and worldwide genus *Cerceris*. Scullen (1968) revised the genus *Eucerceris*, but his key to species and subspecies relied heavily on variable color characters which makes identification of many specimens difficult. Bohart and Grissell (1975) revised the California species, but this helpful work covered only ten of the more than thirty species known. I have undertaken a review of the genus *Eucerceris* with the objective of clarifying synonymy and developing a key to the species based on morphological characters. This paper is the first in a planned series and presents some of the results of these studies.

Eucerceris ferruginosa Scullen (New Status)

Eucerceris ferruginosa Scullen, 1939:45. [Female holotype, Angeles Bay, Baja California Norte, Mexico; Calif. Acad. Sci., San Francisco]; Scullen 1968:30, in part.

Eucerceris baja Scullen, 1948:170. [Male holotype, 20 mi. n. Mesquit, Baja California Norte, Mexico; Calif. Acad. Sci., San Francisco]; Scullen 1968:19; Bohart and Menke 1976:591. *New Synonymy*.

I have studied the three specimens comprising the type series of *Eucerceris ferruginosa* Scullen. The holotype [CAS] and paratype [OSU] from

¹ Oregon Agricultural Experiment Station Technical Paper No. 5717.

Baja California are not the same species as the paratype labelled Mojave Desert n. Palmdale, California, June 22, 1931 (F. E. Lutz) [AMNH]. The latter is the female of *Eucerceris mojavensis* Scullen which is recognized below as a subspecies of *Eucerceris nevadensis* (Dalla Torre). Bohart and Grissell (1975) synonymized both *E. ferruginosa* Scullen and *E. mojavensis* Scullen with *Eucerceris nevadensis* (Dalla Torre) (= *Eucerceris elegans* Cresson)² based on California and Nevada specimens, but the name *ferruginosa* must be applied to the Baja California species as represented by the holotype.

Females of *E. ferruginosa* are essentially all red in body color, but they are morphologically distinct from *E. nevadensis* which also has all red females in a large part of its range. In *E. ferruginosa* the midsection of the clypeus is slightly convex, on about the same plane as the lateral clypeal lobes when viewed in profile, and its apical margin is shallowly biemarginate between the lateral teeth, forming a short, broad, triangular tooth overlying the bases of the pre-apical setae. In *E. nevadensis* the midsection of the clypeus is flat and depressed below the plane connecting the outer margins of the lateral clypeal lobes, and the bases of the pre-apical setae are visible, not being covered by a median tooth.

The holotype and thirteen paratypes of *Eucerceris baja* Scullen have the same collection labels as six females of *E. ferruginosa* Scullen, and five paratypes of *E. baja* have the same collection data as the holotype of *E. ferruginosa*. In addition Scullen (1968) recorded a female of *E. ferruginosa* collected with 12 males of *E. baja* at 28 mi. s.e. El Arco, Baja California [UCB], and I have seen a male and female collected at 33 mi. s. La Laguna, June 30, 1968 [AZS]. These collection records leave no doubt that *E. baja* is the male of *E. ferruginosa*.

This species has been collected at several localities from the vicinity of San Felipe in Baja California Norte to San Carlos in Baja California Sur. One female, possibly adventive, was collected 39 mi. n. Puerto Penasco, Sonora, Mexico [AZS]. Collection dates are from April 1 to September 27 with all intervening months represented except August. This suggests two generations per year. I have seen 24 males, including the holotype of *E. baja*, and 14 females, including the holotype of *E. ferruginosa* [AZS, CAS, CSU, OSU, UCB, UID].

² When Dalla Torre (1890) transferred the species of *Eucerceris* to *Cerceris*, *Eucerceris elegans* Cresson became a homonym of the earlier *Cerceris elegans* Eversmann. He renamed Cresson's species *Cerceris nevadensis* Dalla Torre. Many North American hymenopterists have not recognized the secondary homonymy created by Dalla Torre, and Krombein (1979, 1980) continued to prefer the use of *Eucerceris elegans* Cresson. Bohart and Grissell (1975, p. 27) state that "Although the international rules of nomenclature on this point were changed in 1961, they were not retroactive and the names of . . . Dalla Torre must be used," and I prefer to follow this strict interpretation of the rules as the best long-range policy.

Eucerceris nevadensis nevadensis (Dalla Torre)

Eucerceris elegans Cresson, 1879:xxiii. [Male holotype, Nevada; Acad. Nat. Sci., Philadelphia]; Mickel 1916:413, males only; Scullen 1939:32, males only; Scullen 1965:132.

Cerceris nevadensis Dalla Torre, 1890:200, new name for *Eucerceris elegans* Cresson, nec *Cerceris elegans* Eversmann.

Eucerceris elegans elegans, Scullen 1968:27; Krombein 1979:1739.

Eucerceris elegans monoensis Scullen, 1968:28. [Female holotype, Grant Lake, Mono County, California; Calif. Acad. Sci., San Francisco]; Krombein 1979:1739.

Eucerceris nevadensis, Bohart and Grissell 1975:31, in part.

Eucerceris nevadensis nevadensis, Bohart and Menke 1976:591.

Eucerceris nevadensis monoensis, Bohart and Menke 1976:591.

Bohart and Grissell (1975) synonymized *E. elegans monoensis* with the nominate form and its continued recognition by Bohart and Menke (1976) and Krombein (1979) is apparently due to time lag between copy preparation and final printing of the latter two publications.

E. nevadensis nevadensis occurs in Mono and Inyo Counties, California, and Churchill, Esmeralda, Lyon, Mineral and Washoe Counties, Nevada. It is apparently a Transition Zone form of the eastern slopes of the Sierra Nevada Mountains. I have seen 59 males and 14 females. Collection dates are June 20 to September 27 [AMNH, AZS, CAS, MCZ, OSU, UCB].

Eucerceris nevadensis mojavensis Scullen (New Status)

Eucerceris ferruginosa, Scullen 1939:45, in part, nec holotype; Scullen 1968:30, in part, nec Scullen 1939; Bohart and Grissell 1975:31, nec Scullen 1939.

Eucerceris mojavensis Scullen, 1968:44. [Male Holotype, 7 mi. e. Mojave, California; Univ. of California, Davis]; Bohart and Grissell 1975:31.

Eucerceris nevadensis, Bohart and Grissell 1975:31, in part.

Eucerceris nevadensis ferruginosa, Bohart and Menke 1976:592, nec Scullen 1939.

Eucerceris nevadensis mohavensis (sic), Bohart and Menke 1976:592.

Eucerceris elegans ferruginosa, Krombein 1979:1739, nec Scullen 1939.

The confusion of the females of *E. nevadensis mojavensis* with the females of *Eucerceris ferruginosa* Scullen has been discussed under the latter species. Bohart and Grissell (1975) did not formally recognize subspecies, but they did concede that "a reasonable case could be made for *E. nevadensis ferruginosa* with *mojavensis* as a synonym." Since the name *ferruginosa* Scullen must be used for quite a different species, the name *mojavensis* Scullen is available for this subspecies.

E. nevadensis mojavensis occurs in the Upper and Lower Sonoran Zones of the southwestern states including Inyo, Kern, Los Angeles, San Bernardino and San Diego Counties, California; Mohave and Yuma Counties, Arizona; and Clark, Humboldt, Lincoln and Lyon Counties, Nevada. I have also seen a specimen labelled Cholla Bay, Sonora, Mexico [WSU]. Dates of capture are April 26 to June 28, and August 13 to October 20, indicating the probability of two generations per year. Intergrades occur in Inyo County, California, and Lyon County, Nevada. I have seen 42 males, including the holotype, and 17 females [AZS, AMNH, CAS, OSU, UCB, UCR, USU, WSU].

The following key will separate the two subspecies of *Eucerceris nevadensis* (Dalla Torre):

- 1. Males 2
 - Females 3
- 2. Mesosternum largely or entirely black; anteromedial scutal marks usually small and not fused with the anterolateral marks, sometimes absent *nevadensis nevadensis* (Dalla Torre)
 - Mesosternum largely or entirely white or light yellow; scutal marks always present, usually large and fused with anterolateral marks *nevadensis mojavensis* Scullen
- 3. Ground color of thorax and gaster black, or, at least with large black areas; light colored tergal bands always present *nevadensis nevadensis* (Dalla Torre)
 - Ground color of thorax and gaster red; tergal bands usually absent, but if present, background color red *nevadensis mojavensis* Scullen

Eucerceris lacunosa Scullen

Eucerceris lacunosa Scullen, 1939:19. [Male holotype, Bill Williams Fork, Arizona; Univ. of Kansas, Lawrence].

Eucerceris arizonensis Scullen, 1939:20. [Female holotype, Oslar, Huachuca Mtns., Arizona; Univ. of Kansas, Lawrence].

Eucerceris lacunosa lacunosa, Scullen 1968:34; Bohart and Menke 1976:591; Krombein 1979:1739.

Eucerceris lacunosa sabinasae Scullen, 1968:36. [Male holotype, 23 mi. n. Sabinas, Coahuila, Mexico; Univ. of California, Davis]; Bohart and Menke 1976:591; Krombein 1979:1739. *New Synonymy*.

The slightly darker specimens on which Scullen (1968) based the subspecies *sabinasae* occur sporadically over most of the range of the species. The two color forms are identical morphologically, and therefore no basis exists for maintaining the name *sabinasae*.

I have seen 41 males, including 2 paratypes of *E. sabinasae*, and 12 females. All specimens were within the distribution range given by Scullen (1968). Collection dates ranged from April 23 to September 27 with about 80% of captures in July and August [AMNH, COR, OSU, UAZ, USU].

Eucerceris morula Scullen

Eucerceris morula morula Scullen, 1968:49. [Female holotype, 17 mi. n.e. San Luis Potosi, San Luis Potosi, Mexico; U.S. Natl. Mus., Washington, D.C.]; Bohart and Menke 1976:591; Krombein 1979:1739.

Eucerceris morula albarenae Scullen, 1968:46. [Female holotype, 31 mi. n.e. Las Cruces, Otero County, New Mexico; U.S. Natl. Mus., Washington, D.C.]; Bohart and Menke 1976:591; Krombein 1979:1739. *New Synonymy*.

The two subspecies of *E. morula* were separated by Scullen (1968) on rather tenuous and minor color differences. The tendency toward development of a red or ferruginous color as partial replacement for a black background is commonly encountered in the genus *Eucerceris*. In *E. morula* the tendency is much less pronounced than in such well known species as *E. rubripes* Cresson. Of the large number of specimens studied, no satisfactory basis was found for recognizing subspecies.

I have seen 421 male paratypes and 117 female paratypes of *E. morula morula* as well as 101 male paratypes and 14 female paratypes of *E. morula albarenae* [OSU]. In addition to the distribution given by Scullen (1968), I have seen a specimen from Lincoln County, New Mexico [UID]. Collection dates are from June 15 to October 3 with a strong peak in September.

Eucerceris pimarum Rohwer

Eucerceris pimarum Rohwer, 1908:326. [Female holotype, Phoenix, Arizona; U.S. Natl. Mus., Washington, D.C.]; Bohart and Grissell 1975:32; Bohart and Menke 1976:592; Krombein 1979:1740.

Eucerceris apicata Banks, 1915:404. [Male holotype, Yuma, Arizona; Mus. Comp. Zool., Cambridge, Massachusetts]; tentative synonymy by Bohart and Grissell 1975; synonymy by Bohart in Bohart and Menke 1976.

Eucerceris elegans, Scullen 1939:32, nec Cresson 1879, females only.

Eucerceris pimarum (sic), Scullen 1939:32, as synonym of *Eucerceris elegans* nec Cresson 1879, females only.

Eucerceris pimarum, Scullen 1965:135, females in part; Scullen 1968:52, females in part.

Eucerceris apicata, Scullen 1965:132, males in part; Scullen 1968:11, males in part.

Bohart and Grissell (1975) discussed the confusion surrounding this species and pointed out that the *E. apicata* and *E. pimarum* of Scullen

(1965, 1968) were in fact composed of three species, i.e. *Eucerceris bitruncata* Scullen (= *Eucerceris triciliata* Scullen), *Eucerceris conata* Scullen (= *Eucerceris hespera* Scullen), and *Eucerceris pimarum* Rohwer (= *Eucerceris apicata* Banks).

Distribution of *E. pimarum* is limited to the Lower Sonoran deserts of the southwest, and it is allopatric with both *E. bitruncata* and *E. conata*. Bohart and Grissell (1975) reported *E. pimarum* from Imperial and Riverside Counties, California, and Maricopa, Mohave, Pima and Yuma Counties, Arizona. In addition I have seen specimens from Clark County, Nevada, [USU], and 15 mi. s. Guaymas, Sonora, Mexico [OSU]. The latter is a male without red markings as are some males from the Tucson area in Arizona.

The females of *E. pimarum* were at one time thought to be females of *E. elegans* Cresson, and I have seen 15 males and 11 females standing under the latter name [UAZ]. I have seen a total of 50 males, including the holotype of *E. apicata* Banks, and 40 females of this species. Dates of collection are from May 29 (Clark County, Nevada) to January 10 (Sonora, Mexico) with the bulk of collections in September–October [AZS, CAS, COR, MCZ, OSU, UAZ, UCR, UID, USU].

Eucerceris bitruncata Scullen

Eucerceris bitruncata Scullen, 1939:35. [Female holotype, San Antonio, Texas; U.S. Natl. Mus., Washington, D.C.]; Bohart and Grissell 1975:32; Bohart and Menke 1976:591; Krombein 1979:1738.

Eucerceris triciliata Scullen, 1948:172. [Male holotype, 20 mi. n. El Paso, Texas; Calif. Acad. Sci., San Francisco].

Eucerceris pimarum, Scullen 1965:135, nec Rohwer, females in part, males; Scullen 1968:52, nec Rohwer, females in part, males.

Scullen (1965, 1968) interpreted his *E. pimarum* to include both sexes of *E. bitruncata* as well as females of *E. pimarum* Rohwer, and his (1968) distribution map must be interpreted accordingly. With the exception of the Utah records, which represent an undescribed species to be described separately, all males determined by him as *E. pimarum* belong to *E. bitruncata*.

Peripheral distribution records from the United States are from Cochise and Santa Cruz Counties, Arizona; north through Bernalillo and Guadalupe Counties, New Mexico; Lubbock County, Texas; Cimarron County, Oklahoma; to Barber County, Kansas. It is known from most of the border counties from Hidalgo County, New Mexico, to Cameron County, Texas, and north to Anderson County, Texas. In Mexico it has been collected in the states of Chihuahua, Coahuila, Durango and Zacatecas.

Dates of capture are from May 30 to September 24 in Arizona and New Mexico with a peak in August; from April 14 to October 2 in Texas, Oklahoma and Kansas with a peak in June–July; and from June 24 to October 25 in Mexico with a peak in August. One specimen, a male, from Coahuila,

Mexico, and the single male from Zacatecas, Mexico, are black and white rather than black, yellow and red. I have seen a total of 548 males and 119 females from all parts of the range of the species [AMNH, AZS, CAS, COR, CSU, MCZ, OSU, UAZ, UCB, UCR, UID, USU].

Eucerceris conata Scullen

Eucerceris elegans, Mickel 1916:413, nec Cresson 1879, females only.

Eucerceris conata Scullen, 1939:34. [Female holotype, Halsey, Nebraska; Univ. of Nebraska, Lincoln]; Bohart and Grissell 1975:32; Bohart and Menke 1976:591; Krombein 1979:1738.

Eucerceris hespera Scullen, 1948:171. [Male holotype, 25 mi. e. El Paso, Texas; Calif. Acad. Sci., San Francisco].

Eucerceris apicata, Scullen 1965:132, nec Banks 1915, males in part, females; Scullen 1968:11, nec Banks 1915, males in part, females.

This species has had a tangled history. Mickel (1916) regarded it to be the female of *Eucerceris elegans* Cresson known at that time only from males. Scullen (1939) described *E. conata* for those females referred to *elegans* by Mickel and assigned females to *elegans* that we now know to be *E. pimarum* Rohwer. Scullen (1948) described *E. hespera* suggesting that it might be the male of either *E. bitruncata* or *E. conata*. Scullen (1965) described the true female of *E. elegans* Cresson but incorrectly synonymized *E. conata* and *E. hespera* with *E. apicata* Banks. This interpretation, followed in Scullen (1968), brought together both sexes of *E. conata* and the males of *E. pimarum* under the name *E. apicata* until clarified by Bohart and Grissell (1975).

The distribution data for *E. apicata* given by Scullen (1968) must be revised since *E. pimarum* males were included. The specimens recorded from Pima County, Arizona, are all referable to *E. pimarum* Rohwer, and the specimens recorded from Mono County, California, are over-cyanided males of *E. nevadensis nevadensis* (Dalla Torre) [CAS]. I have not seen the specimen from Coconino County, Arizona.

E. conata occurs in the Wilcox area of northern Cochise County, Arizona, but I have not found it in large quantities of material collected in the Portal area. It has also been collected in Navajo County, Arizona; Grand and San Juan Counties, Utah; Pueblo County, Colorado; Goshen County, Wyoming; Morrill and Thomas Counties, Nebraska; Fall River County, South Dakota; Bernalillo, Chaves, Dona Ana, Lincoln and Socorro Counties, New Mexico; and Culberson and El Paso Counties, Texas. Dates of collection are May 25 to October 7. I have seen two specimens from Samalayuca, in northern Chihuahua, Mexico, collected on June 24 and October 6. I have seen 75 males and 107 females [AMNH, AZS, CAS, CSU, MCZ, OSU, UAZ, UID, USU].

Eucerceris superba Cresson

- Eucerceris superba* Cresson, 1865:108. [Male lectotype, Rocky Mtns., Colorado Territory; Acad. Nat. Sci., Philadelphia].
- Eucerceris fulviceps* Cresson, 1879:xxiii. [Female holotype, New Mexico; Acad. Nat. Sci., Philadelphia].
- Eucerceris bicolor* Cresson, 1881:xxxviii. [Female holotype, Montana; Acad. Nat. Sci., Philadelphia]. *New Synonymy*.
- Cerceris dichroa* Dalla Torre, 1890:199. New name for *Eucerceris bicolor* Cresson, nec *Cerceris bicolor* F. Smith. *New Synonymy*.
- Eucerceris fulviceps* var. *rhodops* Viereck and Cockerell, 1904:84. [Female holotype, Pecos, New Mexico; Acad. Nat. Sci., Philadelphia].
- Eucerceris superba* var. *bicolor*, Scullen 1939:37.
- Eucerceris superba bicolor*, Scullen 1968:65; Krombein 1979:1740.
- Eucerceris superba superba*, Scullen 1968:66; Bohart and Menke 1976:592; Krombein 1979:1740.
- Eucerceris superba dichroa*, Bohart and Menke 1976:592.

Eucerceris bicolor Cresson is a color variant of *Eucerceris superba* Cresson that is known only in females. *E. bicolor* has the posterior terga black, whereas in *E. superba* all terga have broad yellow bands. Scullen (1939) quoted at length from personal correspondence from Prof. O. A. Stevens who had collected the two forms together in North Dakota, and he reduced *bicolor* to the status of a variety. Later (1968) he treated it as a subspecies.

The frequency of the dark form decreases from north to south and from east to west as follows (total females with number of dark form females in parentheses): Alberta 48 (46); Montana 9 (9); North Dakota 17 (16); South Dakota 7 (7); Wyoming 13 (9); Colorado 4 (2, 1 intermediate); Nebraska 4 (4); Kansas 1 (1); Idaho 10 (0); Utah 28 (0); New Mexico 5 (1, 1 intermediate); Arizona 2 (0); Washington 2 (0).

Of interest is the occurrence of this species on Orcas Island (Doebay), San Juan County, Washington. Two males and two females were collected by A. R. Gittins, VIII-14-1964 [UID, OSU]. The females are of the light form. The University of Washington collection is now a part of the collections of the Systematic Entomology Laboratory, Oregon State University, and it is rich in specimens collected on the San Juan Islands and in the Puget Sound area during the early decades of this century. *E. superba* is not represented in that material. The nearest recorded capture is Lewiston, Idaho, (Scullen 1968) near the southeastern border of Washington.

I have seen a total of 127 males and 68 females. Dates of collection are July 2 to September 7 with a pronounced peak in August [COR, OSU, UCB, UCR, UID, USU, WSU].

Eucerceris canaliculata (Say)

- Philanthus canaliculatus* Say, 1823:80. [Male holotype, Arkansas, destroyed; male neotype, Kansas; Acad. Nat. Sci., Philadelphia].
- Cerceris bidentata* Say, 1823:80. [Female holotype, Arkansas, destroyed].
- Eucerceris canaliculata*, Cresson 1865:112; Scullen 1939:47; Bohart and Menke 1976:591; Krombein 1979:1738.
- Eucerceris canaliculata* var. *atronitida* Scullen, 1939:50. [Male holotype, Beaver Canyon, Utah; U.S. Natl. Mus., Washington, D.C.].
- Eucerceris biconica* Scullen, 1948:178. [Female holotype, 15 mi. n. El Paso, Texas; Calif. Acad. Sci., San Francisco].
- Eucerceris canaliculata canaliculata*, Scullen 1968:23.
- Eucerceris canaliculata atronitida*, Scullen 1968:25.
- Eucerceris zimapanensis* Scullen, 1968:72. [Male holotype, 9 mi. n. Ojo Caliente, Zacatecas, Mexico; Calif. Acad. Sci., San Francisco]; Bohart and Menke 1976:592. *New Synonymy*.

Most specimens of *Eucerceris canaliculata* (Say) have yellow markings on a red background, but specimens with a black scutum and black markings on other parts of the body have been collected over much of its range. The dark form from Utah was described by Scullen (1939) under the name *atronitida* and was synonymized by Bohart and Grissell (1975). Scullen (1968) described a similar form as *Eucerceris zimapanensis* from the states of Zacatecas and Hidalgo, Mexico, that had slightly more extensive black markings. The distinction was arbitrary since some specimens from Zimapan, Hidalgo, were determined as *atronitida*. Similar black-marked specimens are common in the states of Durango and San Luis Potosi, Mexico.

With the exception of the Utah population, the frequency of the darker forms increases from north to south. From Dr. Scullen's records I have tabulated some 2,295 specimens determined by him over the years as follows (total specimens shown with number of dark specimens in parentheses): Montana, Wyoming, South Dakota, Nebraska 14 (0); Kansas, Oklahoma, Arkansas 77 (0); Colorado 51 (2); Utah 29 (12); Texas 786 (11); New Mexico 429 (2); Arizona 532 (7); California, Nevada 53 (0); Chihuahua, Coahuila, Nueva Leon 156 (0); Durango 22 (16); Zacatecas 5 (2); San Luis Potosi 125 (75); Queretaro 2 (2); Hidalgo 12 (10); Guatemala 1 (1).

A specimen labelled Puerto Barrios, Guatemala, VIII-16-1965 (Alberto Ortiz) [OSU] extends the known range southward.

A color form occurs in the southwestern deserts in which the terga are entirely yellow, the usual transverse dark stripe of the tergal depressions being absent. I have seen 9 males and 3 females of this form from Imperial, Riverside and San Bernardino Counties, California; Lincoln County, Nevada; and Yuma County, Arizona.

I have seen a total of 561 males, including a paratype of *E. zimapanensis*, and 184 females. Collection dates are from April to October with a broad peak in June, July and August.

Eucerceris lapazensis Scullen

Eucerceris lapazensis Scullen, 1968:37. [Female holotype, La Paz, Baja California Sur, Mexico; Calif. Acad. Sci., San Francisco]; Bohart and Menke 1976:591.

This species is closely related to *Eucerceris canaliculata* (Say) and *Eucerceris sonoreae* Scullen, but the females of *E. lapazensis* are easily separated by the absence of the prominent projections on the lateral lobes of the clypeus characteristic of the other two species. Males of *E. lapazensis* have not heretofore been recognized.

I have examined a series of 8 males and 2 females collected 2 mi. s. La Paz, Baja California Sur, VIII-5/7-1966 that had been previously identified as *E. canaliculata* and *E. lapazensis* respectively [UCB], and a previously unidentified series of 40 males and 6 females collected at La Paz, Baja California Sur, IX-5/7-1967 and IX-17/22-1967 [UCB]. The females are *E. lapazensis* and the males are undoubtedly the same species.

The males of *E. lapazensis* are very close to *E. sonoreae* and *E. canaliculata* in structure and coloration. Most males of *E. canaliculata* can be separated by a rounded, somewhat ridgelike, swelling near the dorsolateral margin of the lateral clypeal lobe that is absent in the other two species. The subantennal sclerite and immediately adjacent areas of the clypeus and lower face are rather sparsely punctate in most specimens of *E. canaliculata* but more densely punctate in the other two species. In *E. lapazensis* the vertex averages somewhat wider with respect to the ocellar triangle than in the other two species. The least vertex width averaged 2.9, 2.8 and 2.7 times the ocellar triangle width in *E. lapazensis*, *E. canaliculata*, and *E. sonoreae* respectively with considerable overlap. I have found no single morphological character which is reliable in all cases for separating the males of these three species. As presently known, the three species are allopatric, and geographic distribution will separate them.

I have seen most of the specimens from Baja California that were determined as *E. canaliculata* by Scullen according to his records. These include the two localities shown in his (1968) distribution map for *E. canaliculata*, and I believe all of his determinations from Baja California are properly referable to *E. lapazensis*.

In addition to the La Paz area, *E. lapazensis* has been collected at Todos Santos, 20 mi. n. Comondu, 20 mi. s. El Arco, and El Centenario in Baja California Sur; and 14 km s. Rosarito and 20 mi. n. Mezquital in Baja

California Norte. I have seen 57 males and 9 females with collection dates from August 2 to October 3. The bulk of the collection dates are in September [CAS, OSU, UCB, UID].

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The Systematic Entomology Laboratory, Oregon State University, contains the extensive collection of cercerine wasps built up by Dr. H. A. Scullen over a period in excess of forty years together with his unpublished notes and records. I have relied heavily on these resources.

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Professor of Entomology, Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, Oregon 97331.

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SOME OBSERVATIONS ON SLOPE SOARING IN
PANTALA FLAVESCENS (ODONATA: LIBELLULIDAE)

David L. Gibo

Abstract.—Slope soaring behaviour is described for the dragonfly *Pantala flavescens* (Fabricius). Some of the physical and airflow properties of a soaring site are also described. The ability to slope soar may have a significant impact on the energy budget of foraging *P. flavescens*.

Powered flight is a highly energetic activity for insects. Because dragonflies perform most of their adult activities in the air (Corbet 1962; Needham and Westfall 1955), any behaviour that reduces the energy expenditure of flight would be advantageous. One pattern of behaviour that can result in a large reduction in energy expenditure is soaring. Soaring occurs when animals extract energy from the atmosphere by gliding in ascending air currents or updraughts. Consequently, soaring animals can maintain or gain altitude without beating their wings.

Rising air currents can be produced by several mechanisms. Updraughts that are produced by convection are termed thermals (Pennycuick 1975; Scorer 1978; Welch et al. 1977), while those produced by wind interacting with an obstacle, such as a hill, are termed slope lift (Pennycuick 1975; Welch et al. 1977; OSTIV 1978).

Although the dispersal of many insects is known to be enhanced by thermals (Johnson 1969; Rainey 1976; Scorer 1978), the specialized behaviour patterns necessary for sustained soaring flight have only been reported for a few species. These species include the monarch butterfly, *Danaus plexippus* L. (Gibo and Pallett 1979; Schmidt-Koenig 1979), the mourning cloak butterfly, *Nymphalis antiopa* L. (Gibo 1981), and the dragonfly *Pantala flavescens* (Fabricius) (Hankin 1921). *Nymphalis antiopa* and *P. flavescens* have only been observed to soar in thermals, while migrating *D. plexippus* exhibit behaviour patterns that allow them to soar in slope lift as well as thermals (Gibo and Pallett 1979). This note is a report of slope soaring behaviour in foraging *P. flavescens* and also describes the physical features of a soaring site.

On August 11, 1980 a *P. flavescens* was observed slope soaring in an area of lift in the lee of a beach house in Kill Devil Hills, North Carolina. The house was on pilings and raised approximately 2 m above the ground. Although air flow under the house was possible, it was impeded both by the pilings and by a lattice work of slats that ran around the perimeter of the pilings. As a result, air flow over and around the house would normally have a

greater velocity than air flow under the house. This flow pattern was apparently producing a form of slope lift in the lee of the house. The exact mechanism may have been due to turbulence (see Munn 1966), a poorly understood three dimensional effect on airflow in the lee of an object (see Scorer 1978), or the Bernoulli principle (see Sears and Zemansky 1970).

The location, dimensions and shape of the area of lift were determined by releasing small bits of paper at appropriate locations and observing whether they were carried upward. The area of lift was located directly in the lee of the house, and was approximately 12 m long, 3 m wide and 2.5 m deep. It was first detectable at approximately 1.5 m above the ground. Wind velocities within the band of lift, and at appropriate locations near the house were measured with a wind meter. The wind direction was from the north. The wind velocity at 1 m was 15 km/hr on either side of the house (approximately 2 m outside the area of lift) and 15 km/hr 1 m above the roof. Directly below the area of lift, at 1 m, the wind velocity was approximately 10 km/hr. The wind velocity within the area of lift, 2 m from the house and 2 m above the ground, was approximately 5 km/hr. The horizontal component of the wind velocity, in this area, was still north (*i.e.* there was no evidence of a counter current). During the observation period the temperature was 24°C and the sky was overcast with broken altocumulus.

The *P. flavescens* was observed from 10:25 to 10:55 A.M. (E.S.T.), while it soared back and forth in the band of lift, generally paralleling the house. The dragonfly tended to fly at a height of approximately 2 m and remain 2 to 3 m from the house. The *P. flavescens* usually soared in a straight line for a distance of approximately 6 m before beating its wings a few times or turning. The duration of the soaring part of the flight was usually 3 s, but ranged between 2–5 s (based on 10 observations). The longer glides extended the entire length of the band of lift. Whenever the *P. flavescens* arrived at the boundaries of the area of lift it made an abrupt 180° turn and usually beat its wings a few times before resuming soaring flight. When the soaring dragonfly was viewed from the front, it could be seen to rock from side to side, indicating that the lift was turbulent.

Occasionally, the *P. flavescens* would suddenly accelerate by beating its wings, and fly 5–10 m in pursuit of small insects. As these flights were usually upward, it was twice possible to observe prey capture against the sky. The dragonfly also employed powered flight to approach other dragonflies that flew near the area, although no overt aggressive encounters were noted. After 30 minutes of observations the dragonfly was collected. Within 10 minutes a second *P. flavescens* flew into the band of lift and began soaring back and forth in the same manner as the first specimen. However, it only remained in the area of lift for approximately 2 minutes.

These observations show that foraging *P. flavescens* are able to locate

and soar in restricted areas of lift. It is important to note that the potential foraging area of a slope soaring dragonfly is larger than the narrow area of lift actually being patrolled. Because air continuously flows through the site, dispersing insects that are upwind of the site may drift towards the dragonfly, extending the effective foraging area.

If the energy metabolism for soaring is similar to the resting metabolism (soaring dragonflies are essentially holding their wings immobile), then slope soaring would substantially reduce the cost of patrolling an area. The relative advantage of slope soaring is indicated by studies of endothermic warm-up in dragonflies. May (1979) found that during warm-up active dragonfly species have maximum metabolic rates, that are approximately 19.5 to 29.5 times higher than their resting metabolism. The expected difference in the two metabolic rates for *P. flavescens* can be calculated from the data presented in May (1979). At 30°C the mean resting metabolic rate, from Table I in May (1979) is 0.0024 W. The mean warm-up metabolic rate, extrapolated from Figure 3 in May (1979) and corrected by the recommended 15%, is approximately 0.0680 W. Consequently, for *P. flavescens*, the metabolic rate during endothermic warm-up is approximately 28 times the resting metabolic rate. If warm-up metabolism approximates flight metabolism, then it is apparent that episodes of slope soaring could be very important in the energy budget and ecology of *P. flavescens*.

Acknowledgments

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Department of Zoology, Erindale College, University of Toronto, Mississauga, Ontario, Canada L5L 1C6.

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A REVISION OF THE GENUS *PEPHYSENA* WITH
DESCRIPTIONS OF TWO NEW SPECIES
(HEMIPTERA: LYGAEIDAE)

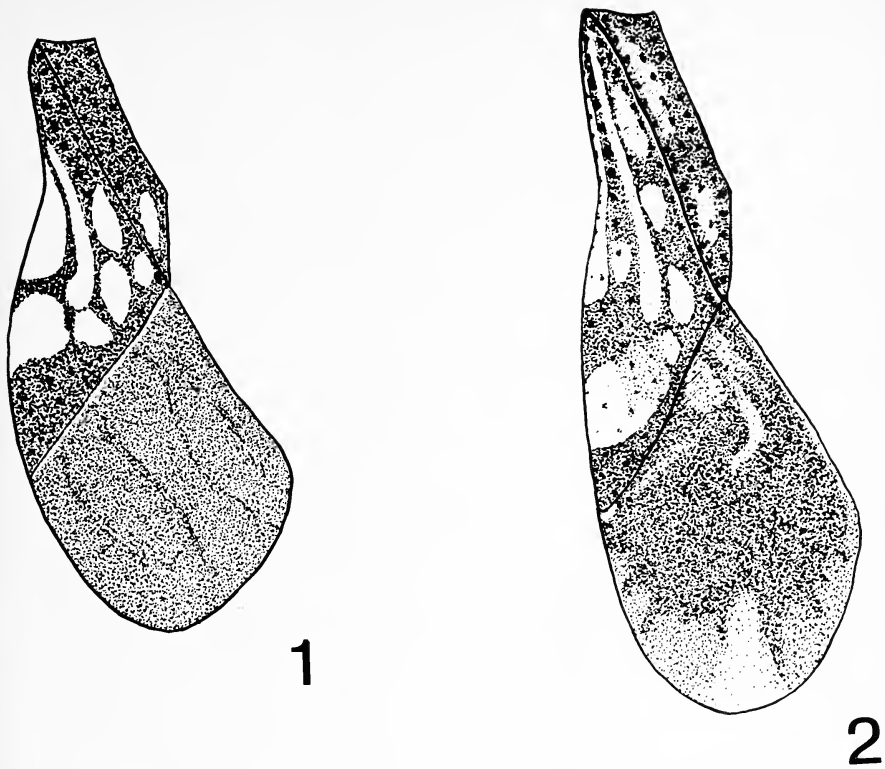
B. J. Harrington

Abstract.—A diagnosis for the Neotropical genus *Pephyse* and a key for identification of five species are presented. Two new species, *P. longirhynchus* and *P. microlevis*, both from Brazil and Surinam are described. Dorsal views of both holotypes are provided.

The Neotropical lygaeid genus *Pephyse* Distant belongs to the tribe Myodochini in the subfamily Rhyparochrominae. Distant's (1882) description of the genus included the description of two species, *P. levis* and *P. insignis*. There was no further taxonomic activity concerning this genus until 1954 when H. G. Barber briefly redescribed *Pephyse*; designated *P. levis* as the type species; noted that *P. insignis* did not belong to the genus *Pephyse*; and described two new species, *P. picta* from Ecuador and *P. fuscata* from Brazil, Trinidad and Venezuela. After examining the type specimen of *P. insignis*, Scudder (1962) removed *P. insignis* to the new monotypic genus *Distingphyses*, which Harrington's (1980) generic level analysis of the tribe Myodochini recognizes as the sister group of *Pephyse*.

Pephyse and *Distingphyses* both have elongate oval eyes, a generally ant mimetic habitus and a unique characteristic texture of nearly contiguous pits or punctures on the head. Yet these two genera are readily distinguishable. *Pephyse* can be recognized by the possession of a long, cylindrical, stalk-like neck; the dome-like convex nature of the head between and immediately behind the eyes; the very long slender antennae (but with the first segment short and not attaining the apex of the tylus); and a markedly impunctate band on the anterior one-third to one-half of the posterior pronotal lobe. *Distingphyses* has the head abruptly constricted behind the eyes but lacks a stalk-like neck; the first antennal segment attains the apex of the tylus; the head is markedly flattened and depressed between the eyes; and the entire posterior pronotal lobe is uniformly punctate. In addition, the lateral corial margin is beaded or crenate for most of its length in *Distingphyses* but smooth in *Pephyse*.

The present paper provides the first key to the species of *Pephyse* including two new species described here from Brazil and Surinam. In the following key and descriptions all measurements are in mm and the Villalobos color chart (Palmer, 1962) has been used as a standard.



Figs. 1, 2. Hemelytral color patterns: 1. *Pephysena fuscosa*, 2. *Pephysena picta*.

Key to Species of *Pephysena*

- 1. Wing membrane entirely and uniformly dark (blackish brown); femora of all legs uniformly dark; ground color of clavus and corium dark, strongly contrastingly marked with white maculae as in Figure 1 *fuscosa*
- Wing membrane, marked mesally or apically with a pale area, or with one or more pale finger-like markings along veins (Figs. 2, 3 and 4); one or more pair of legs with femora pale on proximal one-third to one-half, or all femora entirely light orangish buffy brown or tawny; clavus and corium in part buffy yellow, not marked exclusively in a contrasting black and white pattern 2
- 2(1). Meso- and metafemora uniformly light orangish buffy brown or tawny; wing membrane dark save for a central oval pale spot which is “enclosed” and does not approach posterior wing margin (Fig. 3); head not declivent anteriorly, preocular portion porrect,

- prolonged and snout-like with apex of tylus readily visible from above (Fig. 3) **longirhynchus**
- Meso- and metafemora dark distally and contrastingly pale proximally; wing membrane with pale finger-like markings along veins (Fig. 4) or with a pale median vitta extending forward from posterior margin (Fig. 2); head declivent anteriorly, apex of tylus generally not readily apparent in dorsal view (Fig. 4) 3
 - 3(2). Wing membrane dark on basal (anterior) one-half, lighter on apical (posterior) one-half, with several pale finger-like markings present along veins (Fig. 4) 4
 - Wing membrane without several pale finger-like markings along veins, largely dark, patterned as in Figure 2 with a single pale median vitta extending forward from posterior margin *picta*
 - 4(3). Proximal ends of fore femora dark, concolorous with trochanters; clavus with a slender elongate pale macula adjacent to anterior one-half of claval suture and another elongate pale spot paralleling claval commissure; total length in dorsal view 6.5–8.0 mm *levis*
 - Proximal ends of fore femora pale, contrasting with darker distal one-half to two-thirds of femora and with trochanters; clavus uniformly dark, dusky brown or chestnut, lacking pale slender maculae described above (but with broader heavy gray pruinose light-reflecting patches in the same positions giving a deceptively similar light-marked appearance); total length in dorsal view 4.5–6.0 mm **microlevis**

Pephysema longirhynchus Harrington, new species

Figure 3

Head, anterior pronotal lobe, scutellum basally and laterally and membrane of hemelytra blackish brown; a medial oval spot in membrane and ground color of clavus and corium very pale grayish cream; anterior pronotal collar, posterior pronotal lobe, tylus, juga, femora, tibiae, epimera, episterna, medioapical portion of scutellum and transverse bands on corium at apex and just posterior to claval commissure tawny; tarsi, labium, antennal segment IV, distal portion of segment III and extreme distal end of segment II fuscous; antennal segment I and major portions of segments II and III as well as indistinctly marked areas on clavus and corium between buffy yellow and pale tawny; abdomen light chestnut.

Antennae, legs, labium and abdomen smooth, impunctate and moderately shining; head shining with numerous nearly contiguous micropunctures, this surface reflecting the light in a characteristic broken pattern; pronotum, scutellum and hemelytra including membrane dull, clothed with a pale gray or whitish pruinosity which is densest or most apparent in a broad band across anterior one-third of posterior pronotal lobe; anterior one-third of

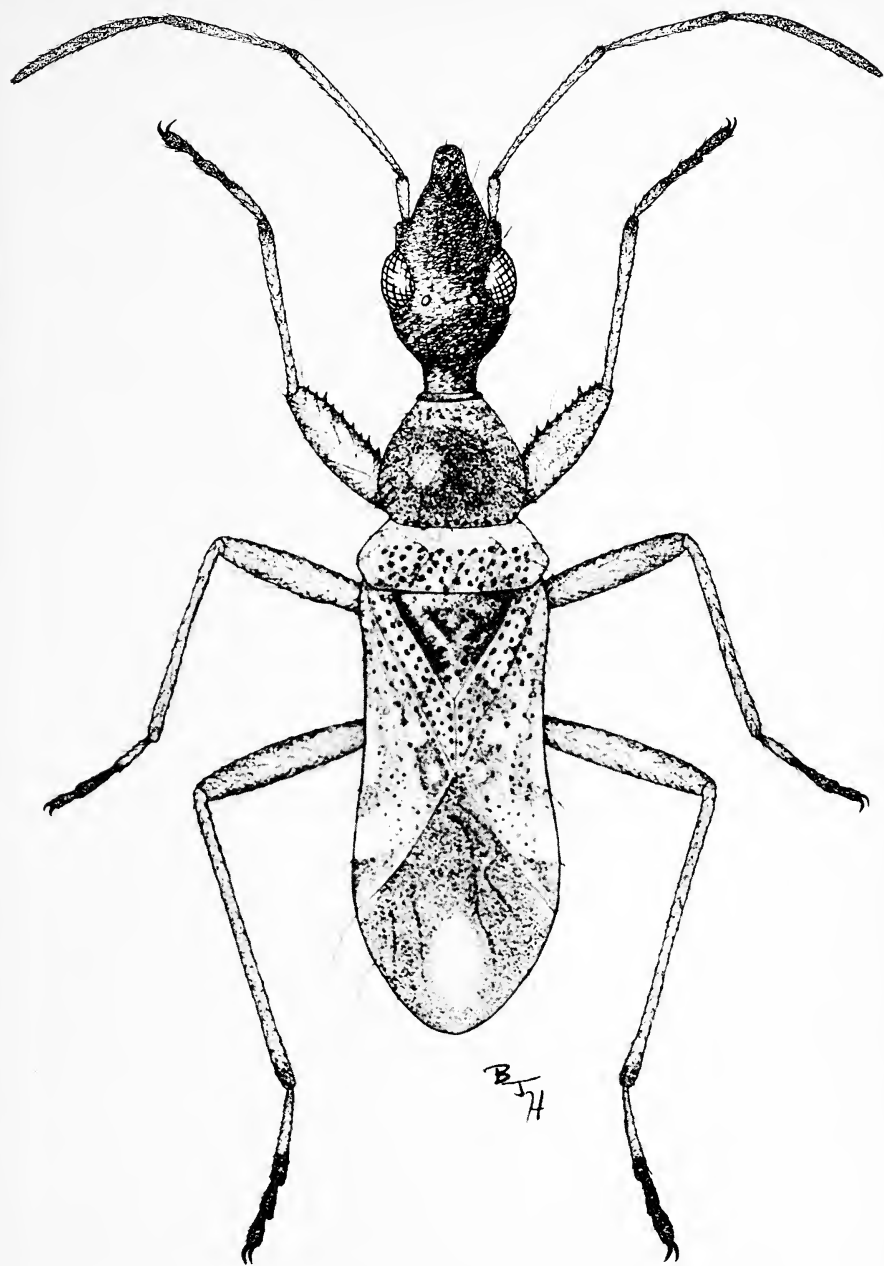


Fig. 3. *Pephysena longirhynchus* Harrington. Holotype, dorsal view.

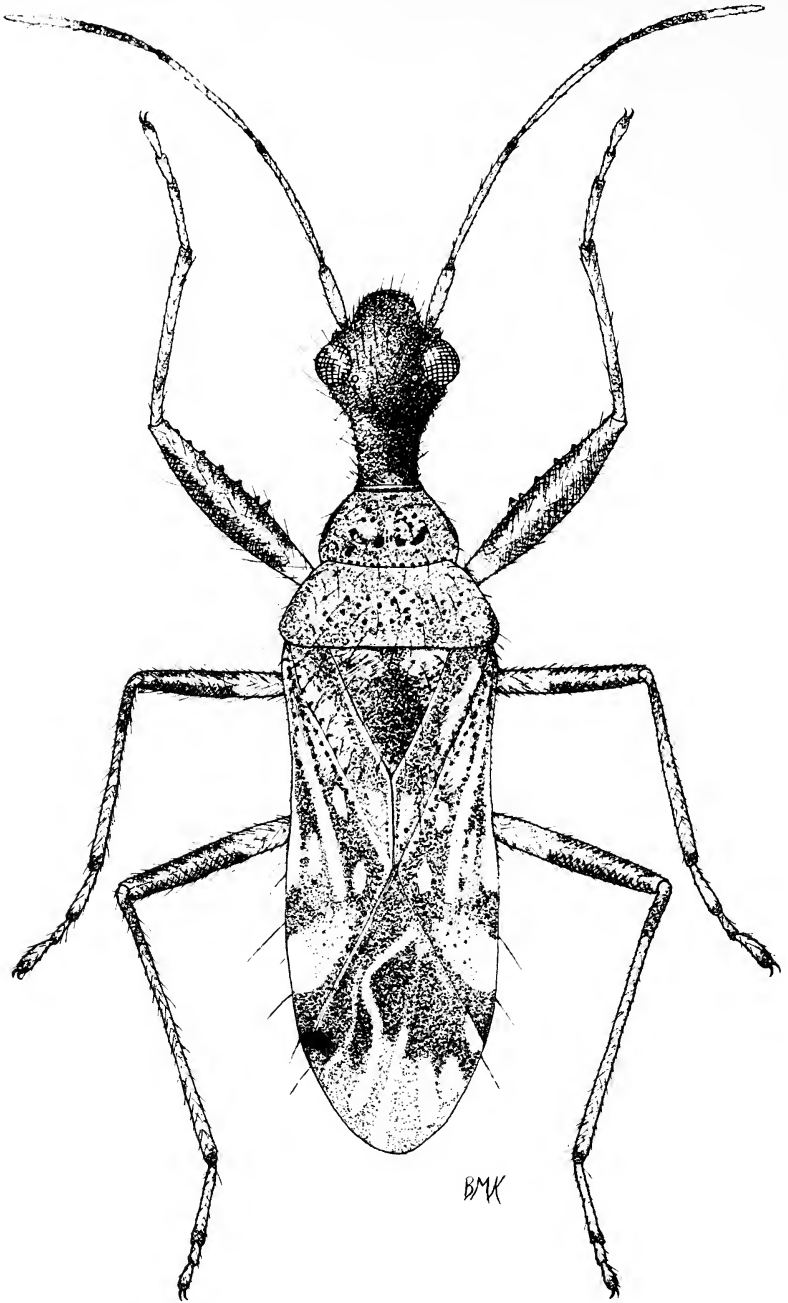


Fig. 4. *Pephysena microlevis* Harrington. Holotype, dorsal view.

posterior pronotal lobe impunctate; anterior pronotal lobe only sparsely punctate with small shallow indistinct punctures; lines or grooves demarking anterior pronotal collar and transverse impression with larger deeper more closely spaced and distinct punctures; punctures equally large or larger on scutellum, clavus, corium and a band across posterior two-thirds of posterior pronotal lobe, excluding wide impunctate lateral areas at the humeral angles (punctures large dark and extremely apparent against light backgrounds of clavus, corium and posterior pronotal lobe); much of body surface, particularly legs and antennae, clothed uniformly with fine short recumbent hairs; fewer long distinctive erect hairs present over entire surface of head, fore femora and scutellum and on dorsal surfaces of both pronotal lobes.

Head little declivent anteriorly with pre-ocular portion prolonged and snout-like; tylus readily apparent in dorsal view; post-ocular region of head elongate, constricted posteriorly to form a stalk-like neck, post-ocular portion of head immediately behind eyes convex and dome-like; eyes sessile, longitudinally oval; length head 1.34; width 0.80; interocular distance 0.46. Anterior pronotal lobe globose, with a distinct anterior collar demarked by a line-like groove; posterior margin of pronotum straight across base of scutellum, humeral angles squarely truncate; length anterior pronotal lobe 0.68; width 0.74; length posterior pronotal lobe 0.40; width across humeral angles 1.02; width transverse impression 0.64. Length scutellum 0.54; width 0.48. Length corium 1.76; distance apex corium to apex membrane 0.72; length claval commissure 0.32; distance apex clavus to apex corium 0.78. Labium extending onto abdominal sternum II (first visible); length labial segments I 0.72, II 0.92, III 0.94, IV 0.38; bucculae quite short but expanded and leaf-like, projecting forward on either side of labial base. Antennae slender; length antennal segments I 0.26, II 0.78, III 0.68, IV 0.88. Total length 4.94.

Holotype: Surinam: ♂ P. H. v. Doesburg Jr. In Leiden Museum No. 1054.

Paratypes: Surinam: 1♂ Same data as holotype. Brazil: 1 (abdomen missing) Mato Grosso 12°15'S, 51°47'W. Campo 16-X-1968, O. W. Richards. In Leiden Museum No. 1056 and J. A. Slater collection.

In the paratype from Surinam the anterior pronotal lobe is lighter than that of the holotype and closer to chestnut in color, hence, contrasting less markedly with the posterior pronotal lobe. In the Brazilian paratype the head is slightly less elongate and a little broader.

P. longirhynchus is quite different from other described species of *Pephysena*. Specimens can be readily identified by the distinctive, pale, medial, oval spot in an otherwise dark wing membrane and the characteristic porrect, prolonged, snout-like preocular portion of the head. In addition, the punctures on the posterior pronotal lobe, scutellum and clavus of *P.*

longirhynchus are larger and deeper than those of other species and are very apparent against a light-colored background.

Pephysena microlevis Harrington, new species

Figure 4

Head blackish brown; anterior pronotal lobe and scutellum dusky brown; anterior one-half of hemelytral membrane fuscous; posterior one-half of membrane smoke gray with distinctive pale gray finger-like markings along veins; posterior pronotal lobe, clavus, broad transverse bands on corium at apex and at level of posterior end of claval commissure and a fine line along entire membranous margin of corium chestnut; coxae, distal one-half to two-thirds of all femora, proximal and distal portions of all tibiae, antennal segment IV, distal one-fourth to one-third of segments II and III, proximal one-half of segment I and abdomen between light chestnut and tawny; other portions of antennal segments and a sinuate vitta along medial fracture in corium buffy yellow; corium narrowly marked with sordid white along lateral margin to level of posterior end of claval commissure, a broad subapical corial macula and three small spots at level of claval commissure (two along claval suture and a third laterad of median fracture) also sordid white; labial segments I, III and IV sepia; segment II sordid buffy yellow; distal end of tarsal segment I and segment II light fuscous; remainder of tarsal segment I, segment II, most of tibial length and proximal one-third to one-half of femur on all legs pale buffy yellow.

Antennae, legs, labium and abdomen smooth, impunctate, moderately shining and evenly clothed with fine recumbent hairs; longer erect hairs present on forelegs, head, scutellum and dorsal surface of pronotum; head shining with numerous nearly contiguous micropunctures, this surface reflecting the light in a characteristic broken pattern; pronotum, scutellum and hemelytra including membrane dull, clothed with a pale gray pruinosity which is densest and most apparent on anterior portion of posterior pronotal lobe, in a pair of patches on base of scutellum and in elongate patches on clavus, one along claval suture at level of scutellum and a smaller one parallel to claval commissure (these areas of heavy pruinosity give a light appearance to and partially mask the actual dark color of the integument beneath); pruinosity of anterior pronotal lobe broken by irregular anastomosing shining spots scattered over calli and by a shining lateral line on propleuron; anterior pronotal lobe very faintly and sparsely punctate laterad; a close row of distinct punctures marking transverse impression; posterior pronotal lobe impunctate on anterior one-third; posterior two-thirds of posterior pronotal lobe (save humeral angles), scutellum and hemelytra distinctly punctate.

Head sharply decurved anteriorly from a dome-like vertex between ocelli; juga and tylus not visible in dorsal view, even antenniferous tubercles barely

visible from above; post-ocular portion of head broad immediately behind eyes, constricted more posteriorly to form a cylindrical stalk-like neck; eyes rounded and protruding; length head 1.00; width 0.94; interocular distance 0.54. Anterior pronotal lobe globose; with a distinct anterior collar demarcated by a line-like groove; transverse impression deeply line-like; posterior pronotal margin straight across base of scutellum, humeral angles rounded; length anterior pronotal lobe 0.46; width 0.70; length posterior lobe 0.40; width across humeral angles 1.12; width transverse impression 0.64. Length scutellum 0.42; width 0.52. Length corium 1.96; distance apex corium to apex membrane 0.74; length claval commissure 0.42; distance apex clavus to apex corium 0.90. Labium extending onto anterior portion of mesosternum, not attaining mesocoxae; length labial segments I 0.50, II 0.50, III 0.32, IV 0.30; bucculae short and rounded, cupped around base of labium. Antennae slender; length antennal segments I 0.36, II 0.78, III 0.72, IV 0.88. Total length 4.70.

Holotype: Brazil: ♂ Natal, Mann. coll. In American Museum of Natural History.

Paratypes: Surinam: 1♂ Paramaribo 26-II-1962 P. H. v. Doesburg Jr. Brazil: 1♀ Taperina; 2♀♀, 3♂♂ Santarem. In Leiden Museum, Carnegie Museum (Acc. No. 2966), J. A. Slater and B. J. Harrington collections.

Color variation in the type series is slight and only one of degree. In several of the paratypes the head is less abruptly decumbent anteriorly than is that of the holotype so that the tylus is apparent in dorsal view.

P. microlevis is closest in appearance to, and might be mistaken for, *P. levis*. However, *P. microlevis* is a smaller species, typically about 5 mm long, with the basal one-third of the fore femora pale and contrasting with the darker distal portion and the clavus uniformly chestnut although marked by two elongate patches of pale gray pruinosity that occur in the same general areas as the actual pale vittae on the clavus of *P. levis*. These features will serve to distinguish specimens of *P. microlevis* from those of *P. levis* which are generally about 7 mm in total length; show distinct pale claval vittae paralleling the claval suture and claval commissure; and have the fore femora not pale at the base but uniformly tawny. In both of these species the proximal one-third to one-half of the meso- and metafemora are pale in contrast to the distal portions.

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Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706.

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AGGREGATION BEHAVIOR OF *APLOMYIOPSIS XYLOTA*
(DIPTERA: TACHINIDAE)

Frank J. Messina

Abstract.—The tachinid *Aplomyiopsis xylota* is a common parasitoid of larvae of *Trirhabda virgata* and *T. borealis* (Coleoptera: Chrysomelidae) in central New York. Flies were observed to aggregate on herbaceous vegetation along the borders between old fields and more shaded habitats (shrubby fields or woodlots). Aggregations comprised from less than one hundred to a few thousand individuals, almost all of which were male. Males continuously perched and moved about in sun flecks on the vegetation, and frequently grappled with each other. In the old field adjacent to the primary aggregation site, the tachinid sex ratio was strongly skewed toward females. Aggregations of *A. xylota* are probably involved in mating.

Tachinid flies in the genus *Aplomyiopsis* Villeneuve parasitize chrysomelid larvae, particularly of the subfamily Galerucinae (Arnaud 1978; D. M. Wood, pers. comm.).¹ The life histories and hosts of most species of *Aplomyiopsis* are unknown. Sholes (1977) obtained an unidentified species of *Aplomyiopsis* from the galerucine *Trirhabda virgata* LeConte. Hogue (1970) reported that several western species of *Trirhabda* were parasitized by *A. xylota* (Curran). During a study of *Trirhabda virgata* and *T. borealis* Blake in central New York, I also found high rates of parasitization of these beetles by *A. xylota*. This paper presents one aspect of the biology of this fly, its aggregation behavior.

Several families of cyclorrhaphous Diptera are known to form adult aggregations (Hunter and Webster 1973; Tychsen 1977). Aggregations typically consist almost entirely of males, in a kind of "waiting station" assembly (Downes 1969). Females are presumed to visit aggregation sites to mate. The site of assembly may be highly specific; certain tachinid species aggregate on mountain summits, hilltops, man-made towers, and other vertical prominences (Chapman 1954; Shields 1967; Lederhouse et al. 1976). I describe here the characteristics of aggregation sites of *A. xylota* and the behavior of individuals in the aggregation.

Methods

Observations were made during 1979-1980 in old fields at the Whipple Farm, 8 km NE of Ithaca, N.Y. (Fig. 1). The vegetation was dominated by

¹ The species *epilachnae* (Aldrich) parasitizes coccinellid larvae, but is no longer placed in *Aplomyiopsis* (D. M. Wood, pers. comm.).

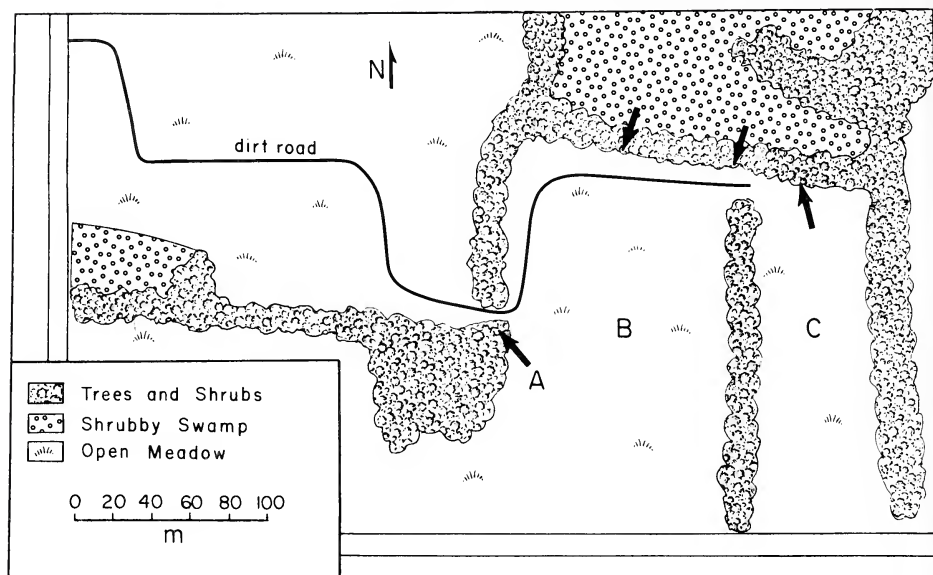


Fig. 1. Map of the Whipple Farm. Arrows indicate aggregation sites. See text for explanation of letter symbols.

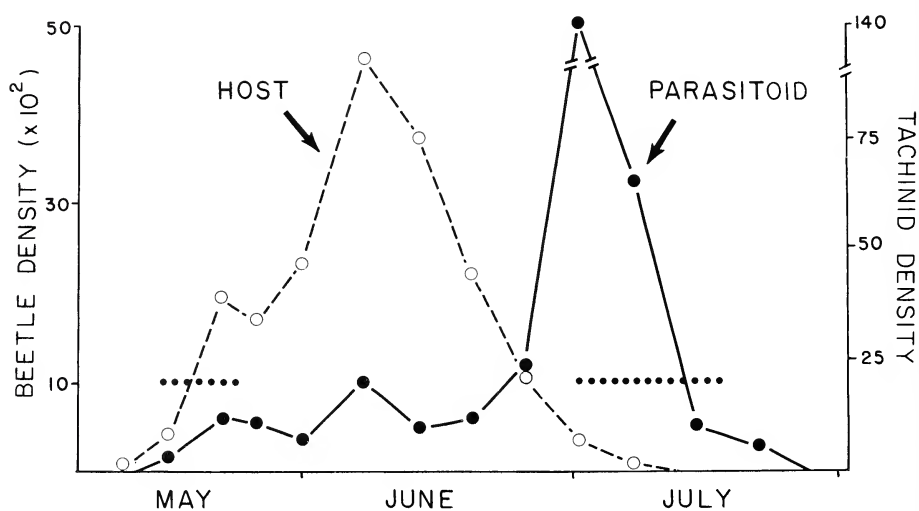


Fig. 2. Seasonal densities (number/100 sweeps) of *Trirhabda* larvae and tachinid adults in 1979. Dotted lines indicate periods when aggregations were observed.

goldenrod (*Solidago* spp.). In 1979, the seasonal abundance of *Aplomyiopsis* adults and *Trirhabda* larvae was estimated by taking weekly sweep samples (100 sweeps/date) along 4 permanent transects (site C in Fig. 1, further described in Messina and Root, 1980). Voucher specimens of the 2 *Trirhabda* spp. and *A. xylota* were placed in the Cornell University Collection in Lot No. 1068.

Results

In 1979, adult flies were first collected in sweep samples in mid-May, shortly after the appearance of their larval hosts (Fig. 2). The tachinid population remained at relatively low density until late June, when flies emerged from *Trirhabda* larvae in peak numbers. Fly density in the old field then declined rapidly, and flies were not found after July.

During 2 periods in 1979 and 1980 (Fig. 2), I observed flies aggregating at several locations along the border between the old field vegetation and the shrubby fields and woodlots (Fig. 1). Aggregations in May were small, consisting of fewer than 50 individuals. Each aggregation occupied an area less than 0.5 m². In late June and July, aggregations were much larger, with several thousand individuals clustered in 2 to 3 square meters at the primary aggregation site (site A in Fig. 1). Flies were clustered on the lower vegetation, which included goldenrod (*Solidago* spp.), aster (*Aster* spp.), Virginia creeper (*Parthenocissus quinquefolia*), poison ivy (*Rhus toxicodendron*), and common barberry (*Berberis vulgaris*). The taller vegetation at the aggregation sites consisted of dogwood (*Cornus* spp.), arrow-wood (*Viburnum* spp.), shadbush (*Amelanchier* sp.), white ash (*Fraxinus americana*), shagbark hickory (*Carya ovata*), black cherry (*Prunus serotina*), and apple (*Pyrus malus*).

Flies were found particularly in the sun flecks on the leaf surfaces at these sites. Individuals alternately perched in the sun flecks, made short, darting flights, and returned to the leaves. Aggregations were maintained throughout the day, and the precise location of the flies changed according to the shifting positions of the sun flecks. In the densest aggregations, flies were tightly clustered, with up to 15 individuals perched on a single goldenrod leaf. A fly in such a cluster frequently oriented toward and lunged onto adjacent individuals. These individuals invariably grappled for an instant and separated. Individuals did not maintain a consistent position in the aggregation. *Vespula* wasps occasionally hovered about and preyed on flies in the aggregation.

On 9 July 1980, 99% of the individuals collected from the primary aggregation site with a sweep net were male (Table 1). A simultaneous sweep sample from several meters away in the open field (site B in Fig. 1) yielded

Table 1. Sex ratio of *A. xylota* populations in the field and laboratory.

	Percent		N	P*
	Male	Female		
Reared from <i>Trirhabda</i> in laboratory	45	55	42	ns
At aggregation site (9 July 1980)	99	1	85	<0.001
At field site (9 July 1980)	15	85	59	<0.001

* Chi-square test.

mostly females. Females in the open field were observed ovipositing on the few remaining *Trirhabda* larvae at this time. Sex determinations of flies emerging from larval hosts in the laboratory indicated a primary sex ratio of 1:1 (Table 1).

Discussion

Male aggregations of *A. xylota* differed from other reported muscoid aggregations (e.g., Lederhouse et al. 1976) in that flies were not clustered at or near the top of any vertical peak. Flies were located on the lower, herbaceous vegetation, and the sites themselves occurred in an area of relatively flat topography. While hilltops usually contain multi-species assemblages (Chapman 1954), only *A. xylota* was observed aggregating at the Whipple Farm sites. It is not known how individuals choose where to aggregate; they may orient toward the relatively abrupt changes in either light intensity or vegetation structure. Individuals clearly respond on a smaller scale to changes in light intensity or temperature by constantly positioning themselves in sun flecks.

Aggregations of *A. xylota* are probably involved in mating; if so, this activity would be spatially separated from host-finding or oviposition. Potential food sources of larval hosts were not available at the primary aggregation site, which produced the most abundant aggregation in each year. The collection of a single female at this site suggests that females do visit it occasionally. The observed lunging and grappling behavior resembled the "trial and error" or "assault" mating behavior of the *Cyclorrhapha* (Thomas 1950; Spieth 1974).

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Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853.

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HESPERIIDAE AS PREY OF *STICTIA CAROLINA*¹

A. Hook

Abstract.—Many dipterous prey records exist for *Stictia carolina* (F.). Only one study reports the use of hesperiids and cicadas in addition to flies as prey items. The present study confirms the use of hesperiids as prey of *S. carolina*; of 9 unicellular nests examined, 4 contained hesperiids in addition to dipterous prey.

Abundant prey records exist for *Stictia carolina* (F.), all but one reporting Diptera, especially Tabanidae. Only Lin (1971) has noted the use of hesperiids (*Atalopedes campestris* Boisduval) and small cicadas, in addition to Diptera, as prey of *S. carolina* (studied in Oklahoma).

This paper confirms the use of HesperIIDae as prey of *S. carolina*. Field research was conducted during Aug 1979, on state forest land, situated 300 m west of Turkey Swamp State Park, Freehold, NJ. Two nesting aggregations, each with 20 to 40 females, were located in small, sandy clearings. Surrounding habitat consisted of a mixed deciduous and evergreen forest (pine barrens type flora).

Females had begun to nest and males were still active when these sites were 1st located on 9 August. Five unicellular nests were excavated on 16 Aug and were found to contain dipterous prey, but 2 cells also had hesperiid wings. Four additional nests excavated on 24 Aug revealed 2 cells bearing skippers and flies. One skipper was determined as *Epargyreus clarus* (Cramer). In 9 nests, 100% contained Diptera while 44% also had hesperiids (1 or 2 skippers per cell).

In the Bembicini, 6 genera are known to prey on HesperIIDae: *Rubrica*, *Stictia*, *Editha*, *Bembix*, *Zyzyx* and *Stictiella* (Evans 1966; Evans et al. 1974; Bohart and Menke 1976). Only in the case of some *Stictiella* do HesperIIDae provide a major source of prey. Lin (1971) suggested that shortage of dipterous prey had led *S. carolina* to select skippers and cicadas in addition to Diptera. Further comparative as well as experimental studies are needed to clarify prey selection in this group.

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Department of Zoology and Entomology, Colorado State University, Ft. Collins, Colorado 80523.

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NOTES ON THE MOTH *PERICOPUS LEUCOPHAEA* WALKER
(LEPIDOPTERA: PERICOPIDAE) AS A DEFOLIATOR OF
THE TREE *VERNONIA PATENS* H.B.K. (COMPOSITAE)
IN NORTHEASTERN COSTA RICA

Allen M. Young

Abstract.—Two closely-spaced individuals of the woody composite *Vernonia patens* H.B.K. were severely defoliated by the brightly-colored, gregarious larvae of the moth *Pericopus leucophaea* Walker (Lepidoptera: Pericopidae) in northeastern Costa Rica. Although many other individuals were examined, no other *V. patens* were found to be defoliated. A group of 66 larvae was found on the larger tree and 20 on the smaller one. At the beginning of a three-day period of observation, about 70% of the larger tree and 40% of the smaller tree was defoliated. Defoliation apparently begins on the lower leaves and spreads towards the top. No larvae disappeared during the study period, suggesting high survivorship. Although individuals of the social paper wasp *Polybia simillima* Smith (Hymenoptera: Vespidae: Polistinae: Polybiini) made repeated attempts to capture larvae, all were unsuccessful. When disturbed by wasps, larvae drop from the plant, either suspending themselves on silken threads or falling into the dense undercover. Larvae thus dislodged successfully relocate the plant as they are capable of very rapid locomotion. When prodded with forceps, larvae exhibit strong thrashing movements and exude droplets of a clear fluid which may have a defensive function. Both the aposematic appearance and behavior of the larvae (and adults) suggest unpalatability. Unusually attractive conditions of individual plants, and high survival of egg masses and larvae, probably promote defoliation. Various factors are predicted to determine intensity of defoliation and comprise a basis for further study of this interesting system.

Vernonia patens H.B.K. is a locally abundant woody composite of secondary-growth habitats in the premontane and lowland tropical wet forest regions of northeastern Costa Rica. This small tree (canopy about 4–5 meters tall) of woody shrub often grows as small clumps or single individuals in regenerating fields and along the edges of forest, habitats where it is used as a feeding and chorusing site for various species of cicadas (Homoptera: Cicadidae) (Young 1980a, b). The purpose of this brief communicate is to report the severe defoliation of two individuals of this tree species by the gregarious larvae of the medium-sized (i.e. wingspan of 40 mm) moth *Pericopus leucophaea* Walker (Lepidoptera: Pericopidae) in this region of Costa



Fig. 1. The larger of the two *Vernonia patens* (Compositae) defoliated by the gregarious larvae of the moth *Pericopus leucophaea* (Lepidoptera: Pericopidae) at one site in northeastern Costa Rica, February 1981. Note the severe defoliation of the lower branches of this tree and the relatively intact crown of young leaves. When disturbed by *Polybia* wasps the aposematically-colored larvae drop off the tree into the dense ground cover below, and then crawl back to the same plant.

Rica during the dry season. The general pattern of defoliation of the two trees, and the ineffectiveness of a social paper wasp, *Polybia simillima* Smith (Hymenoptera: Vespidae: Polistinae: Polybiini) as a predator on the larvae of this species, are described for the first time.

Methods

On 3 February 1981, I discovered two closely-spaced *Vernonia patens* trees, one about 1.5 meters tall and the other about 2.5 meters, in different stages of noticeable defoliation by the gregarious larvae of an unidentified moth species. The location of these trees, about 3 meters apart, is along a gravel road at "Finca La Tigra," near La Virgen (10°23'N, 84°07'W; 220 m. elev.), Heredia Province, Costa Rica. The habitat is a road-side patch of regenerating secondary vegetation, and no other individuals of *V. patens* were found within 20 meters in any direction from this "island." Between 3 and 5 February, I made daily observations on the number of larvae present, their behavior, the amount of defoliation of each tree, and the interaction of the larvae with other arthropods. I checked the two trees at various times each day, to determine larval feeding patterns, if any, and changes in the location of larvae on the trees. A sample of 20 larvae was collected the evening of 5 February and confined, along with fresh cuttings of the food plant, to a clean, clear-plastic bag, for rearing to the adult stage since I had to leave the site at this time. The captured larvae were taken to other sites in Costa Rica, until 25 February, at which time they were taken to Milwaukee, Wisconsin (as pupae) to complete the rearing.

At several times during the field study, the larvae were prodded with forceps to elicit defensive behavior.

Results

At the time of discovery, approximately 70% of the leaves from the larger of the two trees had been stripped from the trees (Fig. 1), and about 40% of the leaves of the smaller tree were gone. That the leaves had been eaten by the larvae was verified by examining the number of chewed petioles, and distinguishing these from regular leaf-drop.

Based on voucher specimens of larvae, pupae, and adults, the moth was identified later as *P. leucophaea*. No other lepidopterous larvae were found on the trees, and with the exception of an occasional orthopteran, no other herbivorous insects were found during daytime hours. A brief inspection of an additional 20 individuals of *V. patens* of similar size, scattered over the site, failed to turn up additional larvae of *P. leucophaea*. At the time of discovery the larvae were easy to spot from a distance of about 5 meters with unobstructed view from the road, owing to their bright color patchwork



Fig. 2. Gregarious behavior and defoliation by larval *Pericopus leucophaea*. Left: cluster of larvae, forming a conspicuous mass (to the human observer) amidst the defoliated branches of the food plant and just below the crown. Right: the larvae form tightly-packed aggregations on branches, petioles, and leaf midribs, bared by defoliation.

of red, white and black, and their gregarious habit (Fig. 2). At this time the larvae were about 15 mm long. During the three days of observation, there were 66 larvae on the larger tree, and 20 on the smaller tree.

Larvae feed intermittently throughout the day, but become very quiescent by 5:30 p.m. As many as ten *Ectatomma* ants were seen crawling over the leaves of each tree during this study, sometimes on the same leaves where larvae were resting or feeding. The ants did not attack the larvae. Defoliation apparently started near the bottom of the tree since the crown of each tree was largely intact (Fig. 1), and most of the *Ectatomma* were found on these young leaves.

Tight clusters of larvae were seen on defoliated petioles and leaf midribs (Fig. 2), rendering them very conspicuous to the human eye. When resting in clusters (Fig. 2), individual larvae, when gently poked with a forceps, exhibit rapid thrashing movements of the anterior half of the body, and produce small clear droplets, which were first noticeable on some of the

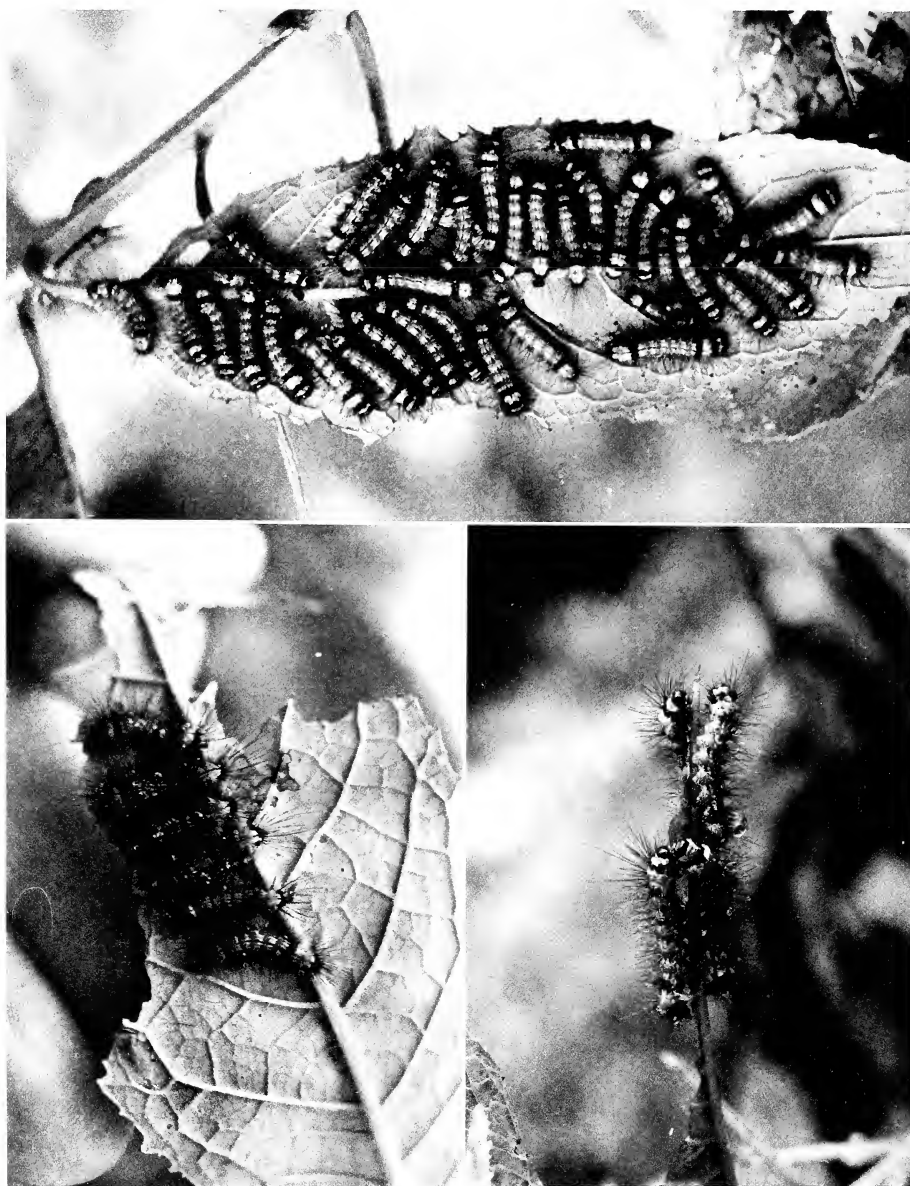


Fig. 3. Gregarious feeding and defensive behavior by the larvae of *Pericopus leucophaea*. Top: a typical larval aggregation on the underside of a mature leaf of *Vernonia patens*. The light areas on the bodies of the larvae are bands of white and orange interspersed with bands of black. Below, left: gregarious feeding. Below, right: the larva in full view at the top has just exuded a large droplet of clear fluid on the dorsal bristles just before the posteriorly-terminal segments. This fluid may have a defensive function.

long hairs of body segments (Fig. 2). Sometimes clusters of many larvae were seen on the undersides of leaves, and such leaves were usually quickly defoliated (Fig. 3). The positions of groups varied greatly each day, presumably as a result of feeding activity. Sometimes there were both solitary larvae and several small clusters (Fig. 3) on the larger tree.

On 4 February, I observed from 1 to 3 individuals of the polybiine wasp *Polybia simillima* make repeated attempts to capture larvae, either ones in clusters or single individuals. From a total of 45 predatory-attack attempts observed, none was successful. On a typical attack, a wasp would weave among the leaves and upon discovering one with larvae on it, it would then land on the dorsal side of the leaf, crawl a bit, and then quickly flip over to the ventral side to capture a larva. But at the moment the wasp landed, most of the larvae dropped off the leaf, some suspended on long silken threads, while others (most) fell into the dense herbaceous layer beneath the tree. For a total of twelve larvae followed after falling into the dense cover on different occasions, each one returned to the food plant. The larvae crawl very rapidly when disturbed, and one dislodged from the food plant is usually back on it within five minutes after a fall. Larvae suspended on threads usually dropped to the ground and then crawled to the food plant.

Deliberate mechanical disturbance of larvae on leaves with forceps does not elicit the "dropping off" behavior. In the larger group of larvae, there were two sized classes apparent, the larger sub-group of 45 individuals being about 15 mm long, and the smaller ones, about 10 mm long. All individuals in the group of twenty on the smaller tree were the same size (20 mm long).

In captivity, larvae pupated about 18 days after discovery, each one forming a loose cocoon wrapped in a leaf. The pupa stage lasted about 18 days in this study.

By the end of the field study, both trees were almost entirely defoliated, save for small crown areas of young leaves on each one. Since it required more than two additional weeks to bring larvae to pupation, both trees would have been insufficient total food supply for the larvae under natural conditions.

Discussion

The defoliation of individual food plants by a herbivorous insect species in the tropics may be considered an "outbreak" if a large portion of the local food plant population is defoliated. The defoliation of a few individuals of such a population, however, may be a result of isolated patches where survival of the herbivore is unusually high, and may not necessarily be an "outbreak." A variety of ecological factors, including the degree to which

patches of varying size of a plant species experience severe defoliation, determine pest outbreak conditions in the tropics (e.g., Rey et al. 1981).

While the present study on the interaction of *P. leucophaea* with *V. patens* is very preliminary, the data suggest that defoliation of a few closely spaced individuals of the food plant resulted from an "escape" of a few egg clusters of the moth from regulatory agents such as predators and parasitoids. There is, however, a growing body of evidence showing that the early stages of Lepidoptera are sources of prey for a variety of arthropods (e.g., Gilbert and Singer 1975).

There have been very few studies of pericopid moths anywhere, save for some systematic and survey studies (e.g., Kendall 1970, 1974; Beutelspacher 1976) and very little is known about the food plant associations of individual species within and outside of the tropics. Presumably the moth places large egg clusters on the food plant, and upon hatching, the larvae exhibit pronounced gregariousness as shown in the present study. Studies of noctuid and arctiid moths feeding on *Vernonia* species indicate considerable food plant specificity in terms of species exploited (e.g., Tietz 1951; Burnett et al. 1974). To the human observer, the brightly-colored larvae of *P. leucophaea* and their gregarious behavior on the food plant suggest aposematic display and unpalatability. Some *Vernonia* contain high concentrations of bitter sesquiterpene lactones in the leaves (Abdel-Baset et al. 1971; Mabry et al. 1975), which could be the basis for suspected unpalatability of some herbivores such as *P. leucophaea* if these compounds are incorporated into the insects. These compounds have also been demonstrated to be a basis for oviposition preferences in various Lepidoptera exploiting some species of *Vernonia* (Burnett and Jones 1978).

Because sesquiterpene lactones in some *Vernonia* have been shown to deter feeding by some Lepidoptera (Burnett et al. 1974), the aposematic coloration of both the larvae and adult stages of *P. leucophaea* may be indirect evidence that this species is able to sequester and incorporate these compounds. Relative to what is known about the feeding-detering properties of these compounds for other Lepidoptera (Burnett et al. 1974), and assuming these compounds to be present in the age-classes of leaves of *V. patens* exploited by larval *P. leucophaea*, this moth may have entered into a new adaptive zone (in the context of Ehrlich and Raven 1965). The vivid color pattern of the adult moths, with wings banded in black, white, and red, not only suggests unpalatability, but also mimetic resemblance to female *Parides* (Lepidoptera: Papilionidae: Papilioninae: Troidiini) found in the same habitats (e.g., *P. iphidamas*—see Young 1977b). Adult *P. leucophaea* fly during the daytime and could possibly participate in a Mullerian mimicry association with these *Aristolochia*-feeding butterflies, even though the moths are somewhat smaller than typical female *Parides*.

The association of *P. leucophaea* with *V. patens* in Costa Rica may be a very specific interaction. It would be expected that a group-feeding brightly-colored herbivore such as *P. leucophaea* would have evolved effective defense mechanisms against predators and parasitoids. My preliminary observations on the ineffectiveness of the wasp *P. simillima* to successfully capture the larvae supports the contention of effective defenses being operative. Thus, in addition to the suspected systemic unpalatability, the composition and functional role of the observed droplets of fluid exuded by the larvae when prodded warrants further study in this context.

A plausible working hypothesis for detailed study of the *P. leucophaea* \times *V. patens* interaction in Costa Rica may be that individual egg masses, if escaping from predation or parasitism, result in large groups of larvae which generally have high survival on the food plant. Although *Polybia* wasps at this locality are successful at capturing the gregarious larvae of the butterfly *Mechanitis isthmia* Bates (Lepidoptera: Ithomiidae) on *Solanum* spp. (Solanaceae) (Young 1978), presumably the larvae of *P. leucophaea*, although also gregarious, have an effective means of making *Polybia* attacks very unsuccessful, if my observations are representative of such interactions. In the *Mechanitis* study, *Ectatomma* was also present in close proximity to the larvae, and neither attacked the larvae nor provided an effective defense against the *Polybia* attacks. In the present study, the effectiveness of *P. leucophaea* larvae in escaping from *Polybia* attacks appears to be intrinsic to the larvae, with *Ectatomma* having no apparent effects on the interaction.

When egg and larval survival is high, defoliation of individual food plants may occur. The severity of such defoliation will be a function of the effective size of the egg masses on each individual plant (i.e., the number of eggs hatching) and the physiological receptivity of the individual plant to the larvae. As shown by my preliminary data, smaller numbers of larvae on a plant result in less damage than larger numbers on a larger plant. For *P. leucophaea*, egg masses are presumably placed on lower leaves since the defoliation begins at the bottom of the plant and spreads upwards. As my observations were made in the short and erratic dry season of this region, the possibility exists that conditions resulting in localized defoliation of *V. patens* may be seasonal.

The ability of the larvae of *P. leucophaea* to crawl very rapidly may allow them to encounter other individuals of the food plant when defoliation is severe.

Under conditions of relaxed predation or parasitism on eggs and larvae, one consequence of massive group-feeding is the rapid defoliation of the food plant. Enforced emigration to fresh plants, made possible by high locomotory ability, allows the larval population to re-distribute on the food plant population.

Since *V. patens* often occurs in clumps of varying sizes abundant over relatively small areas of habitat, when conditions are favorable for the survival of large numbers of eggs and larvae, larval dispersal behavior and successful encounter of fresh food plants may prevent localized extinctions.

In the tropics in particular, defoliation by herbivorous insects should be considered as highly transient and ephemeral conditions associated with changes in food plant distribution, community structure, and kinds of control mechanisms operative on populations (e.g., Rey et al. 1981). The degree to which an individual of *V. patens* will be defoliated by *P. leucophaea* is therefore directly related to a wide variety of factors, including (a) attractiveness of the individual for oviposition by the moth and numbers of egg masses deposited, (b) survival patterns of eggs and larvae, (c) effects of other herbivores on this *individual* plant, (d) the dispersal strategy of mated female moths, (e) the degree of oviposition preference for *V. patens*, and (f) the effects of seasonality on (a–e), if any. A complete understanding of severe defoliation of plants other than crops in the tropics requires a consideration of these factors. Such factors determine the carrying capacity of the environment at any one point in time for herbivores such as *P. leucophaea* on *V. patens*.

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Department of Invertebrate Zoology, Milwaukee Public Museum, Milwaukee, Wisconsin 53233.

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BOOK REVIEWS

Fleas. Proceedings of the International Conference on Fleas, Ashton Wold, Peterborough, U.K., 21-25 June 1977. R. Traub and H. Starcke, eds. A. A. Balkema, Rotterdam. 1980. 420 pp. \$49.50.

This book is unique in several aspects. Beautifully published, with 150 black and white illustrations, it represents the first multiauthor treatise on fleas (Siphonaptera), one of the most important groups of vectors of human and animal disease agents. The list of contributors reads like who is who in flea research, and even like who *was* who because it starts, properly, with a very interesting and personal chapter devoted to Nathaniel Charles Rothschild (1877-1923), the foremost conservationist, collector of fleas and author of 150 scientific publications (more than 100 dealing with fleas), who did his scientific work "in his spare time" while working for the Rothschild banking house. His famous daughter, the world's renowned authority on fleas, Dr. Miriam Louisa Rothschild, herself the author of more than 250 scientific papers, together with her son, Dr. Charles Lane, hosted the 80 participants of the international conference at Ashton Wold.

The first two chapters (pp. 13-172), by Prof. Traub, deal with new genera of Siphonaptera and with adaptive modifications in fleas. The excellent illustrations, prepared by the author, are very well reproduced in these chapters, documenting the convergent evolution and flea taxonomy. Following chapters, of various lengths, reflect the extensive experience of the authors and the high level of excellence in the area of flea research. R. L. C. Pilgrim describes fleas of New Zealand. The New World host associations of *Pulex* are dealt with by Cluff E. Hoppla. James R. Busvine illustrates his chapter on the four Fs (fleas, fables, folklore and fantasies) with drawings of diverse flea traps that I found most interesting and amusing. The control of flea vectors of plague is described by Norman G. Gratz. Ecological interrelationships among fleas are covered by D. C. Cavanaugh and J. E. Williams. Harry Hoogstral describes flea vectors of rickettsiae and trypanosomes. Flea studies in the U.S.S.R. are reviewed by V. A. Bibikova and I. F. Zhovtyi, and a link between epizootics of sylvatic plague in California and caves in the Lava Beds National Monument are outlined by B. C. Nelson and C. R. Smith. Excellent electron micrographs of rickettsiae in the flea midgut are provided by S. Ito and J. W. Vinson. The role of flea vectors in murine typhus, tularemia, and myxomatosis are the subjects of shorter reports. J. Goose describes chemical control of fleas and Rachel Galun the specificity and biological significance of the feeding response. The last 16 contributions, two in French, deal with flea physiology, morphology, behavior and taxonomy. The presentation of each facet of a chapter is clear,

lucid, and to the point. Those desiring detailed information on fleas will find for the first time in a single volume a complete up-to-date survey of the subject.

This book will appeal to a very wide audience. I recommend it highly for use in entomology departments and in medical schools.

Karl Maramorosch, *Waksman Institute of Microbiology, Rutgers—The State University, New Brunswick, New Jersey.*

An Atlas of the Fleas of the Eastern United States. Allen H. Benton. Marginal Media, Fredonia, N.Y. 1980. 177 pp. 63 maps. Looseleaf, Soft Cover. \$6.50.

The book was designed to facilitate the study of the geographic distribution of the fleas of the eastern United States by permitting the qualified reader to spot the known records and to readily add and map new data as they appear.

There are a few introductory pages on the 'natural history and ecology' of fleas and an outline of the history of Siphonapteran studies for the area. A checklist of the fleas of the eastern U.S. is presented ahead of the atlas of 63 pages of maps, on which dots are used to indicate the known records, arranged by county. A set of larger maps near the front of the book shows the counties for the states encompassed. A glance at the maps suffices to grasp the known information on any of the species regarding its distribution within the region in question. For each species listed, the author also provides a summary of available information on hosts, seasonal abundance, and medical importance. One or two references are cited in each case as sources for additional data. Pertinent state and regional references and some general ones, are cited at the end of the book, preceding an appendix on the distribution of the fleas of Minnesota. This book does not purport to be a guide for the identification of fleas, nor is it a taxonomic work in any sense of the term. Not even the original descriptions are cited.

The author worked diligently and accurately in checking references and in tracking down and verifying certain critical specimens. None of the species known to occur in the territory seem to have been omitted, and the scientific names used agree with the standard literature. The comments on bionomics and seasonal variations for the various species will be appreciated by all who have had to comb scattered references seeking such meaningful information. The appendix has valuable ecological notes on Minnesota.

The manner in which the book is organized presents problems for the reader. The list of species included in the atlas (pp. 24–26) is arranged by family and subfamily, but there is no indication of the pages where the

particular maps and discussion are to be found. The species are not arranged alphabetically (even by family) in the list or in the sequence of maps, and it is difficult to find the appropriate page one seeks, even if he is familiar with the scheme of classification and the system used. The sequence employed is based upon that employed by Hopkins and Rothschild in the Catalogues or by R. E. Lewis in his host-lists, but the Catalogue series had indices and Lewis' papers were arranged alphabetically and hence are easy to use. Benton apparently relies upon the maps to indicate what he means by "eastern United States," but the territory included does not have ecological or natural boundaries. Minnesota is treated, but not Iowa, Mississippi, Arkansas and Louisiana, all of which have a western boundary that is east of that of Minnesota. If Minnesota were not discussed, it could be stated that the book was restricted to the states east of the Mississippi River. The appendix on Minnesota is somewhat confusing regarding its bibliographic citation, since the authors are not designated. By checking the bibliography it can be deduced that the 'senior author' mentioned here and there in the text is Benton, and the 'junior author,' R. Timm.

There are inherent disadvantages in any atlas on fleas because of the inadequacy of available data. Even in the U.S. there are vast areas where little or no collecting has been done. In consequence, many species-maps may unavoidably mislead the non-specialist into believing that the blanks represent the absence of species instead of the absence of data. Many of the fleas listed seem to be found only near certain university-towns harboring entomologists or mammalogists. The following example illustrates the problem. Bird-fleas would be expected to have a broad range, considering the extent of the territory covered by their hosts (both as species and as individuals) but *Ceratophyllus celsus* is listed only from four states and in three widely-separated areas.

The author must have been thinking of the U.S. and Canada when he wrote "Flea students are extremely fortunate in having the entire literature in their field quite well presented in a few excellent sources." The statement does not apply to Asia, South America, etc. The notes on medical significance refer to the species in general and not merely to the eastern part of this country. For example, unless the reader realizes that plague does not occur in the east, he can be misled. It is regretted that no conclusions, generalizations or interpretations of the data are presented, and that there is no discussion of zoogeography, for example. It also would have been edifying to compare the range of the host with that of its fleas. Thus, pocket gophers occur in Georgia and Florida, but their characteristic fleas are unreported south or east of Illinois and western Indiana. Unfortunately, the format employed precluded the presentation of data to substantiate the remarks. *Nosopsyllus fasciatus* is stated to be "most abundant in the summer." but is this true throughout the eastern U.S. or only in the north? The species has been considered a flea of temperate zones and the impression

exists that in many areas *N. fasciatus* is most common in cool weather.

This book will be extremely useful to those who are interested in reviewing, compiling, or adding to data on the Siphonapteran fauna of the eastern United States, or who want access to more information on those species. It should also serve to encourage research along those lines, which would be a boon, for a real need exists for such endeavors.

Robert Traub, *Department of Microbiology, University of Maryland School of Medicine, Baltimore, Maryland.*

Leafhopper Vectors and Plant Disease Agents. K. Maramorosch and K. F. Harris, eds. Academic Press, 111 Fifth Avenue, New York, NY 10003. 1979. 654 pp. Price \$42.00.

This text, a companion volume to the excellent treatise on *Aphids as Virus Vectors*, is part of a planned series on vectors and vector-borne diseases. It is organized into the following five parts: Part I includes two chapters on the taxonomy and bionomics of leafhoppers; Part II, three chapters on the worldwide importance of leafhoppers and planthoppers as vectors; Part III, four chapters on vector-disease agent-plant interactions; Part IV, five chapters on experimental approaches to virus-vector and MLO-vector research; and Part V concludes the volume with five chapters on the leafhopper transmission of specific viruses and prokaryotes. These last chapters give detailed information on rice viruses and MLOs and control of their vectors, corn stunt, western X-disease, and xylem-borne plant pathogens.

Excellent reviews of leafhopper vector research have been contributed by 25 authorities from eight countries. Many of the chapters are much more than organized reviews or summaries of current research. The authors have made a special effort to draw conclusions based on their own experiences and have raised questions that hopefully will stimulate others to make further contributions to leafhopper vector research. The text includes a number of useful illustrations of good quality and many valuable summary tables.

Although information in portions of this text have appeared in past review-type texts and series, this particular collection of papers will be an excellent addition to the library of anyone concerned with vectors and vector-transmitted plant diseases. The editors are to be congratulated on putting together a coherent volume with minimum duplication in spite of the numerous contributors. The extensive lists of key references make this text of great value to teachers of advanced entomology and plant pathology courses.

E. H. Varney, *Department of Plant Pathology, N.J. Agricultural Experiment Station and Rutgers University.*



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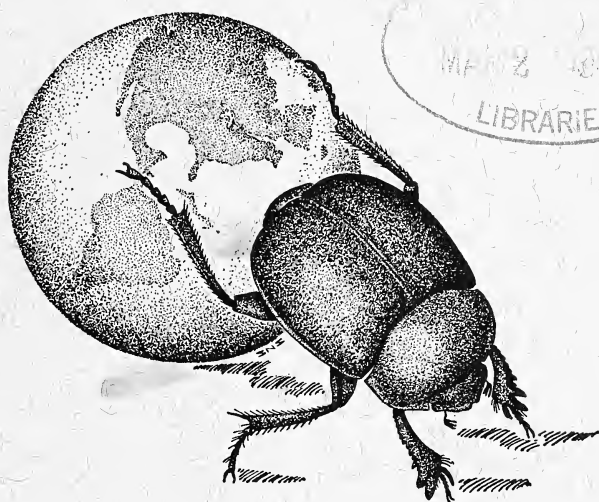
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A WORLD CATALOG OF GENERA ASSOCIATED
WITH THE GLYPHIPTERIGIDAE AUCTORUM
(LEPIDOPTERA)

John B. Heppner

Abstract.—The catalog lists 272 generic-group names previously associated with the family Glyphipterigidae auctorum of the world and segregates these generic names to Glyphipterigidae sensu stricto (Copromorphoidea), Immidae (Immoidea), and Brachodidae and Choreutidae (Sesioidea), as well as 21 other families. Transfers to other families are based on examination of the type-species of each genus, in some cases only on literature references and notes from colleagues. Generic synonyms, homonyms, and type-species, with their designations, type localities and depositories, are given when known. Lectotypes are designated for 19 of the generic type-species listed. A complete bibliography is given for all included taxa, as well as an index to cited species. V. O. Becker contributes the new name, *Rectiostoma* Becker, replacing *Setiostoma* Zeller, 1875 [not *Setiostoma* Felder and Rogenhofer, 1875] in Oecophoridae (Stenomatinae).

The following catalog lists generic names previously associated with the family Glyphipterigidae auctorum and reassigns them to appropriate families. Included are generic names originally described in Glyphipterigidae, names subsequently transferred to the family, and generic names at one time or another associated with the family. The Glyphipterigidae auctorum was a family concept largely the result of generic and family groupings by Edward Meyrick, a British lepidopterist active from 1875 until 1938. Meyrick's (1914d) concept of the family encompassed what had often been considered two families prior to this century, Glyphipterigidae and Choreutidae. These two families, as well as numerous other groups, Meyrick combined into one chaotic family based upon morphological similarities and a general superficial similarity in wing maculation, as far as various metallic iridescent markings are concerned. These two families have more recently again become recognized as distinct, in fact belonging to different superfamilies, Copromorphoidea for Glyphipterigidae and Sesioidea for Choreutidae (Heppner 1977a). In addition, further segregation of some genera has been completed to form the family Immidae (Heppner 1977a) and a revised Brachodidae, formerly Atychiidae (Heppner 1979a; Heppner and Duckworth 1981).

This catalog notes the current family position of 272 generic names (including synonyms and misspellings) previously associated with the Gly-

phipterigidae auctorum. Many genera have been found to belong to a wide range of families, in fact a total of 24 families other than Glyphipterigidae, including the following:

Acrolepiidae	Immidae
Agonoxenidae	Incurvariidae
Brachodidae	Limacodidae
Choreutidae	Noctuidae
Copromorphidae	Oecophoridae
Douglasiidae	Plutellidae
Elachistidae	Psychidae
Epermeniidae	Pyalidae
Gelechiidae	Tineidae
Geometridae	Tortricidae
Gracillariidae	Yponomeutidae
Heliodinidae	Zygaenidae

The catalog is largely the result of investigations of generic type-species completed in conjunction with a revision of the North American Glyphipterigidae and Choreutidae. In beginning the generic studies it quickly became apparent that a review of the world genera associated with the Glyphipterigidae auctorum would be needed, both to determine the actual parameters of Glyphipterigidae sensu stricto and Choreutidae, and also to properly define each family in relation to other families, especially the recently defined families of Brachodidae and Immidae.

Although all the type-species of genera herein restricted to Glyphipterigidae, Brachodidae, Choreutidae, Immidae, and the tribe Hilarographini of Tortricidae (a group especially well associated with choreutids for a long time) were studied, not all the type-species of other genera listed have likewise been studied. Some type-species were not examined because in many cases well known genera were involved and there was no further need to verify their family placement, although at some previous time they were associated with the Glyphipterigidae auctorum. In only a few cases were literature references or notes of colleagues relied upon, in some cases due to inability to locate the holotypes for genera based upon uniques.

As presently restricted, out of a total of 272 generic names listed, 42 names remain in Glyphipterigidae sensu stricto, 24 names remain in Immidae, 22 names remain in Brachodidae, and 62 names remain in Choreutidae. These names are summarized and listed briefly for each family below. The families as now perceived contain 1,016 described species: 326 in Glyphipterigidae (Heppner 1982c), 238 in Immidae (Heppner 1982b), and 96 in Brachodidae and 356 in Choreutidae (Heppner 1981a).

Glyphipterigidae (Copromorphaidea)

- Chrysocentris Meyrick, 1914
Irinympha Meyrick, 1932
Ernolytis Meyrick, 1922
Carmentina Meyrick, 1930
 Metapodistis Meyrick, 1933
Cotaena Walker, [1865]
Myrsila Boisduval, [1875]
Lepidotarphius Pryer, 1877
 Desmidoloma Erschoff, 1892
Tetracmanthes Meyrick, 1925
Phalerarcha Meyrick, 1913
Cronicombra Meyrick, 1920
Taeniostolella Fletcher, 1940
 Taeniostola Meyrick, 1920, preocc.
Machlotica Meyrick, 1909
 Maclotica [sic] Busck, 1915, missp.
Abrenthia Busck, 1915
Neomachlotica Heppner, 1981
Trapeziophora Walsingham, 1892
Ussara Walker, 1864
 Setiostoma Felder and Rogenhofer, 1875
 Usara [sic] Busck, 1933, missp.
Electrographa Meyrick, 1912
Rhabdocrates Meyrick, 1931
Apistomorpha Meyrick, 1881
Phryganostola Meyrick, 1881
Pantosperma Meyrick, 1888
Circica Meyrick, 1888
Glyphipterix Hübner, [1825]
 Heribeia Stephens, 1829
 Aechmia Treitschke, 1833
 Aecimia [sic] Boisduval, 1836, missp.
 Glyphipteryx Zeller, 1839, emend.
 Glyphiteryx [sic] Fischer von Röslerstamm, 1841, missp.
 Anacampsoides Bruand, 1850, nom. oblit.
 Glyphopteryx Herrich-Schäffer, 1854, emend.
 Glyphiptoryx [sic] Mann and Rogenhofer, 1878
 Glyphptieryx [sic] Turati, 1879, missp.
 Glyphipterys [sic] Christoph, 1882, missp.
 Glyphyteryx [sic] Hampson, 1918, missp.
 Glyphteryx [sic] Watt, 1920, missp.
Diploschizia Heppner, 1981

Immidae (Immoidea)

- Ptochaula Meyrick, 1920
Bursadella Snellen, 1880
 Scaptesylix Hampson, 1895, n. syn.
Cercosimma Diakonoff, 1948
Alampla Diakonoff, 1978
Moca Walker, 1863
 Adricara Walker, 1863, n. syn.
 Alicadra Walker, [1866], n. syn.
 Jobula Walker, 1866, n. syn.
 Callartona Hampson, [1893], n. syn.
Bryonympha Meyrick, 1930
Sthenistis Hampson, 1896
Loxotrochis Meyrick, 1906
Birthana Walker, [1865]
 Methypsa Butler, 1875, n. syn.
 Hyperperissa Walsingham, 1900, n. syn.
Imma Walker, [1859]
 Pingrassa Walker, [1859]
 Tortricomorpha C. Felder, 1861
 Topaza Walker, 1864
 Vinzela Walker, [1866]
 Thylacopleura Meyrick, 1886
 Davendra Moore, 1887
 Pseudotortrix Turner, 1900

Brachodidae (Sesioidea)

Brachodinae

- Brachodes Guenée, 1845
 Chimaera Ochsenheimer, 1808, preocc.
 Atychia Latreille, 1809, preocc.
 Procerata Berthold, 1827, nom. oblit.
 Chimera [sic] Feisthamel, 1833, missp.
 Palamernis Meyrick, 1906
 Bradyptesis sensu Kasy, 1979
Miscera Walker, 1863
Euthorybeta Turner, 1913
Synechodes Turner, 1913
Atractoceros Meyrick, 1936
Callatolmis Butler, 1877
 Sisyroctenis Meyrick, 1936

Sagalassa Walker, 1856
Gora Walker, 1862
Jonaca Walker, 1863
Polyphlebia Felder, 1874

Phycodinae

Phycodes Guenée, 1852
Tegna Walker, 1866
Nigilgia Walker, 1863
Nigilica [sic] Turner, 1929, missp.
Hoplophractis Meyrick, 1920

Choreutidae (Sesioidea)

Brenthiinae

Litobrenthia Diakonoff, 1978
Brenthia Clemens, 1860
Microaethia Chambers, 1878

Choreutinae

Anthophila Haworth, [1811]
Simaethis Leach, 1815
Xylopoda Berthold, 1827
Xylopoda Latreille, 1829, redesc.
Simoethis [sic] Desmarest, 1848, missp.
Symaethis [sic] Bruand, 1850, missp.
Xylopodo [sic] Morris, 1872, missp.
Simaetis [sic] Kautz, 1930, missp.
Simethis [sic] Bleszynski, Razowski, and Zukowski, 1965, missp.
Antophila [sic] Bleszynski, Razowski, and Zukowski, 1965, missp.
Siamethis [sic] Klimesch, 1968, missp.
Millieria Ragonot, 1874
Ripismia Wocke, [1876]
Rhipismia Reutti, 1898, emend.
Milliereia Spuler, 1910, emend.
Milliera [sic] Le Marchand, 1937, missp.
Millieroa [sic] Le Marchand, 1937, missp.
Peotyle Diakonoff, 1978
Prochoreutis Diakonoff and Heppner, 1980
Choreutis of authors [not Hübner, 1825]
Prochoreutis Heppner, 1981, redesc.
Caloreas Heppner, 1977
Tebenna Billberg, 1820

- Porpe* Hübner, [1825]
Tebeuna [sic] Danilevsky, 1969, missp.
Asterivora Dugdale, 1979
Asterophaga Horning and Greenwood, 1977, nom. nud.
Choreutis Hübner, [1825]
Hemerophila Hübner, [1806], rejected
Eutromula Frölich, 1828
Choreutes Treitschke, 1835, emend.
Macropia O. Costa, [1836]
Chorentes [sic] Morris, 1871, missp.
Entomoloma Ragonot, 1875
Chorentis [sic] Turner, 1898, missp.
Orchemia sensu Fernald, 1900
Hemerophila sensu Fernald, 1900
Choreutidia Sauber, 1902
Allononyma Busck, 1904
Allonyma [sic] Fracker, 1915, missp.
Cloreutis [sic] Kautz, 1930, missp.
Choreuthis [sic] Hackman, 1947, missp.
Chloreutis [sic] Viette, 1948, missp.
Allonomyia [sic] Ferguson, 1975, missp.
Saptha Walker, 1864
Badera Walker, 1866
Chordates Snellen, 1877
Choredates [sic] Pagenstecher, 1884, missp.
Saphtha [sic] Walsingham, 1900, missp.
Tortyra Walker, 1863
Choregia Felder and Rogenhofer, 1875
Choregia Zeller, 1877, redesc.
Hemerophila Hübner, [1817]
Gauris Hübner, 1821
Walsinghamia Riley, 1889
Guaris [sic] Fernald, 1900, missp.
Zodia Heppner, 1979
Melanoxena Dognin, 1910
Rhobonda Walker, 1863

Family Distribution of Other Genera

Incurvariidae

- Tegeticula* Zeller, 1873
Thia H. Edwards, 1888, preocc.
Thelethia Dyar, 1893, repl. name

Tineidae

Ereunetis Meyrick, 1881

Psychidae

Aprata Moore, 1883

Cebysa Walker, 1854

Sezeris Walker, 1863

Colpotorna Meyrick, 1920

Taleporia Hübner, [1825]

Gracillariidae

Callisto Stephens, 1834

Euprophantis Meyrick, 1921

Philodoria Walsingham, 1907

Oecophoridae**Depressariinae**

Callizyga Turner, 1894

Autostichinae

Lasiodictis Meyrick, 1912

Xyloryctinae

Amphimelas Turner, 1929

Mylocera Turner, 1897

Symphorostola Meyrick, 1927

Stenomatinae

Aproopta Turner, 1919

Rectiostoma Becker, 1982, repl. name

Setiostoma Zeller, 1875, preocc.

Oecophorinae

Aeolocosma Meyrick, 1881

Coridomorpha Meyrick, 1914

Eretmocera Zeller, 1852

Staintonia Staudinger, 1859

Heliostobes Zeller, 1874

Hierodoris Meyrick, 1912

Homoplastis Meyrick, 1926

Lamprystica Meyrick, 1914

Lygronoma Meyrick, 1913

Pachyphoenix Butler, 1883
Tyriomorpha Meyrick, 1918
Mattea Duckworth, 1966

Hypertrophinae

Allotropha Diakonoff, 1954
Epithetica Turner, 1923
Eupselia Meyrick, 1881
Hypertropha Meyrick, 1881
Oxytropha Diakonoff, 1954
Peritropha Diakonoff, 1954
Polygiton Diakonoff, 1955

Elachistidae

Perittia Stainton, 1854

Agonoxenidae

Chrysoclista Stainton, 1854
Glyphipteryx Curtis, 1827, nom. oblit.
Heinemannia Wocke, 1853
Tebenna Hübner, [1825], preocc.

Gelechiidae

Dichomeris Hübner, [1825]
Rhobonda Walker, 1864, preocc.
Carna Walker, 1864, repl. name; preocc.

Copromorphidae

Lotisma Busck, 1909
Ordrupia Busck, 1911
Ardrupia [sic] Busck, 1911, missp.
Ordupia [sic] Busck, 1911, missp.

Epermeniidae

Agiton Turner, 1926
Picrodoxa Meyrick, 1923

Plutellidae

Araeolepia Walsingham, 1881
Ellabella Busck, 1925
Probolacma Meyrick, 1927
Spilogenes Meyrick, 1938

Homadaula Lower, 1899

Homadaula Meyrick, 1907, redesc.

Paraprays Rebel, 1910

Stichotactis Meyrick, 1930

Napecoetes Turner, 1913

Protosynaema Meyrick, 1886

Yponomeutidae

Charixena Meyrick, 1920, repl. name

Philpottia Meyrick, 1916, preocc.

Charizena [sic] Neave, 1939, missp.

Ditrigonophora Walsingham, 1897

Embryonopsis Eaton, 1876

Iridostoma Meyrick, 1909

Niphonympha Meyrick, 1914

Calantica Zeller, 1847, preocc.

Piestoceros Meyrick, 1907

Roeslerstammia Zeller, 1839

Tanaoctena Turner, 1913

Nesotropha Turner, 1926

Cylicophora Turner, 1927

Douglasiidae

Klimeschia Amsel, 1938

Tinagma Zeller, 1839

Douglasia Stainton, 1854

Acrolepiidae

Acrolepia Curtis, 1838

Antispastis Meyrick, 1926

Heliodinidae

Actinoscelis Meyrick, 1912

Amphiclada Meyrick, 1912

Corsocasis Meyrick, 1912

Encratora Meyrick, 1923

Epicroesa Meyrick, 1907

Lithariapteryx Chambers, 1876

Philocoristis Meyrick, 1927

Sobareutis Meyrick, 1910

Thrasydoxa Meyrick, 1912
Thriambeutis Meyrick, 1910
Trichothyrsa Meyrick, 1912

Tortricidae

Olethreutinae

Cryptophlebia Walsingham, 1899
 Thaumatotibia Zacher, 1915
Cydia Hübner, [1825]
 Orchemia Guenée, 1845
Dudua Walker, 1864
Ganabalia Diakonoff, 1975

Chlidanotinae

Archimaga Meyrick, 1905
Charitographa Diakonoff, 1979
Embolostoma Diakonoff, 1977
Hilarographa Zeller, 1877
Idiothauma Walsingham, 1897
Irianassa Meyrick, 1905
Mictocommosis Diakonoff, 1977
Mictopsichia Hübner, [1825]
 Mictopsychia [sic] Riley, 1889, missp.
 Mictropsichia [sic] Heppner, 1978, missp.
Nexosa Diakonoff, 1977
Thaumatographa Walsingham, 1897
 Hilarographa sensu Meyrick, 1886
 Tharmatographa [sic] Diakonoff, 1977, missp.

Zygaenidae

Adscita Retzius, 1783
 Atychia Ochsenheimer, 1808
 Atichia [sic] Ochsenheimer, 1808, missp.
 Bradyptesis Sodoffsky, 1837
Burlacena Walker, [1865]
 Sesiomorpha Snellen, 1885
Cibdeloses Durrant, 1919

Limacodidae

Penthocrates Meyrick, 1934

Pyralidae

Heliothela Guenée, 1854

Orosana Walker, 1863

*Oroso*na [sic] Cotes, 1889, missp.

Geometridae

Menophra Moore, 1887

Hemerophila Stephens, 1829, preocc.

Noctuidae

Chalenata Walker, 1864

Porphyrinia Hübner, [1821]

Anthophilae Hübner, [1806], rejected

Antophila Hübner, [1806], rejected

Anthophila Ochsenheimer, 1816, preocc.

Anthophyla [sic] Duponchel, 1829, missp.

Anthrophila [sic] Treitschke, 1832, missp.

Heliomanes Sodoffsky, 1837

Thopelia Nye, 1975, repl. name

Plotheia Walker, 1863, preocc.

Discussion of Selected Genera

1. *Agiton* Turner, 1926: newly transferred to Epermeniidae. The morphological characters of this genus are amenable to the family Epermeniidae, namely a naked haustellum, absence of ocelli and chaetosemata, small maxillary palpi, smooth head vestiture, upcurved labial palpi with an elongated middle segment (typical for the family), wing venational characters, and bristles on the hind tibiae (typical for the family). The abdominal articulation is not typical for Copromorphoidea, as it appears rather of the tortricoid type, however, there are elongated ventral sclerotized rods on the anterior sternite but these do not actually reach the apodemes as is normal in the tineoid form in Copromorphoidea.
2. *Allotropa* Diakonoff, 1954: newly transferred to Oecophoridae by relational characters conforming to other genera of the Hypertrophinae.
3. *Antispastis* Meyrick, 1926: newly transferred to Acrolepiidae due to genital and wing venational characters typical for this family, e.g., the long male genital saccus and the enlarged aedeagus, both unique to Acrolepiidae among the Yponomeutoidea.
4. *Aprata* Moore, 1883: this genus conforms to Psychidae, as Moore originally noted.
5. *Araeolepia* Walsingham, 1881: transferred to Plutellidae by Heppner

- (1978a) by virtue of head morphology, among other characters, conforming to this family.
6. *Burlacena* Walker, [1865]: transferred to Zygaenidae. This genus is a typical tropical zygaenid and why it was placed in Glyphipterigidae is difficult to comprehend. There is no relationship to Yponomeutidae as alluded to by Common (1970b).
 7. *Cebysa* Walker, 1854: transferred to Psychidae by Common (1970b). This genus conforms to other tropical psychids, although it is unusual.
 8. *Cercosimma* Diakonoff, 1948: tentatively transferred to Immidae. The described characters appear to conform to the family definition of Immidae (Heppner, 1977a, 1982b) but the unique holotype (supposedly in the RMNL collection) has not been located.
 9. *Charixena* Meyrick, 1920: newly transferred to Plutellidae. Meyrick's original description of *Philpottia* Meyrick (1916), a homonym replaced by *Charixena*, is quite detailed and notes the reduced labial palpi and minute haustellum, among other characters. There may be some relationship between this genus and such genera as the Japanese *Rhabdocosma* and *Bhadorcosma* but *Charixena* is otherwise quite isolated in the family.
 10. *Cibdeloses* Durrant, 1919: transferred to Zygaenidae. Like *Burlacena*, this is a typical tropical zygaenid.
 11. *Colpotorna* Meyrick, 1920: newly transferred to Psychidae. This genus was originally allied to *Cebysa* Walker, now in Psychidae, and its characters appear to conform to this group of unusual Australian psychids.
 12. *Coridomorpha* Meyrick, 1914: newly transferred to Oecophoridae by virtue of a scaled haustellum and long upcurved labial palpi, among other characters.
 13. *Cotaena* Walker, [1865]: transferred to Glyphipterigidae by Heppner (1981a). This genus includes species subequal to the largest known glyphipterigids and otherwise conforms to certain tropical members of the family. It has no relation to Heliodinidae, as thought by Naumann (1971).
 14. *Ditrigonophora* Walsingham, 1897: tentatively transferred to Yponomeutidae. The two known specimens of the type-species both lack heads and abdomens. However, these parts were apparently intact when Walsingham described the species and from his description it appears that the moths may have some affinity to yponomeutids like *Xyrosaris*, which also have the unusual distally enlarged labial palpi noted by Walsingham.
 15. *Ellabella* Busck, 1925: transferred to Plutellidae by Heppner (1978a). This genus has no relation to Glyphipterigidae and is in fact a senior synonym of *Spilogenes* Meyrick, 1938, both conforming to Plutellidae.
 16. *Encratora* Meyrick, 1923: newly transferred to Heliodinidae. The short porrect labial palpi and naked haustellum are typical of Heliodinidae.

17. *Epicroesa* Meyrick, 1907: newly transferred to Heliodinidae. The genus has labial palpi and other head morphology typical of tropical Heliodinidae.
18. *Epithetica* Turner, 1923: newly transferred to Oecophoridae. This genus is a member of the Hypertrophinae (Common, pers. comm.).
19. *Heliosibes* Zeller, 1874: newly transferred to Oecophoridae. This genus is typical for Oecophoridae and why it was associated with Glyphipterigidae by Meyrick (1914d) is difficult to understand.
20. *Hierodoris* Meyrick, 1912: newly transferred to Oecophoridae. This genus also is a typical oecophorid among a group of New Zealand genera related to *Heliosibes*.
21. *Hilarographa* Zeller, 1877: transferred to Tortricidae by Diakonoff (1977a) and Heppner (1977a). As noted by Heppner (1978a), the naked haustellum and unusual genitalia relate this genus and its relatives to other Chlidanotinae.
22. *Homadaula* Lower, 1899: transferred to Plutellidae by Friese (1962). There is no question that this genus is not a choreutid by virtue of a naked haustellum and tineoid abdominal articulation, the latter placing the genus outside of Sesioidea. It also is not related to Brachodidae by virtue of this same articulation. There also are no characters to support a placement in Copromorphoidea, or Glyphipterigidae in particular, but rather a placement among some other tropical plutellids is amenable to the characters of the genus. *Homadaula* is an unusual tropical plutellid, although now introduced into some temperate regions, and appears related only to *Prays* to any degree. It may require a separate subfamily but since the tropical Yponomeutoidea as a whole are so poorly known, considerable research is yet required to determine its true nearest relatives.
23. *Homoplastis* Meyrick, 1926: newly transferred to Oecophoridae. The unique holotype has not been located. Meyrick's notation that the genus appears related to *Eupselia* prompts a transfer to Oecophoridae pending further study.
24. *Irianassa* Meyrick, 1905: newly transferred to Tortricidae. This genus conforms to characters of other Hilarographini (Chlidanotinae).
25. *Iridostoma* Meyrick, 1909: transferred to Yponomeutidae by Heppner (1981a). This genus has a naked haustellum and other characters placing it in Yponomeutidae.
26. *Lamprystica* Meyrick, 1914: newly transferred to Oecophoridae. The scaled haustellum and long labial palpi are typical of Oecophoridae and conform, together with other characters, to the Stathmopodini.
27. *Lotisma* Busck, 1909: transferred to Copromorphidae by Heppner (1978a). This genus has an array of characters, notably genital features and wing venation, that align it with other copromorphids.

28. *Loxotrochis* Meyrick, 1906: newly transferred to Immidae. This genus appears to conform to characters of Immidae but should be studied further whenever it is rediscovered (indeed the type locality should be reconfirmed as well).
29. *Lygronoma* Meyrick, 1913: transferred to Oecophoridae by Heppner (1981a). This genus has a scaled haustellum and shows other characters placing it in Oecophorinae (Becker, pers. comm.).
30. *Melanoxena* Dognin, 1910: transferred to Choreutidae by Heppner (1981a). This genus has a scaled haustellum and wing venation similar to other choreutids and appears very near to *Rhobonda*.
31. *Mictopsichia* Hübner, [1825]: transferred to Tortricidae by Diakonoff (1977a) and Heppner (1977a). This genus appears to be related to other Hilarographini but needs further study to verify a possible relationship to Archipini (Tortricinae).
32. *Myrsila* Boisduval, [1875]: transferred to Glyphipterigidae by Heppner (1981a). This genus has no relationship to Sesiidae, (Eichlin, pers. comm.) as originally thought by Boisduval ([1875]), but conforms to certain tropical glyphipterigids, notably *Cotaena*.
33. *Napecoetes* Turner, 1913: newly transferred to Plutellidae. This genus appears to conform to other plutellids, perhaps nearest *Plutella* (Common, pers. comm.), but is still known only from the unique holotype.
34. *Nesotropha* Turner, 1926: newly transferred to Yponomeutidae as a junior synonym of *Tanaoctena* Turner, 1913, as confirmed by Common (pers. comm.).
35. *Pachyphoenix* Butler, 1883: newly transferred to Oecophoridae. This genus is the senior synonym of *Tyriomorpha* Meyrick, 1918, and *Mattea* Duckworth, 1966, and conforms to characters for Oecophorinae (Becker, pers. comm.).
36. *Penthocrates* Meyrick, 1934: newly transferred to Limacodidae. Although transferred to the Zygaenoidea by Meyrick (1934) as a member of the Heterogynidae, the genus appears more typical of the Limacodidae.
37. *Philcoristis* Meyrick, 1927: newly transferred to Heliodinidae. The genus exhibits the short porrect labial palpi and other characters typical of tropical Heliodinidae. It may be related to *Epicroesa*.
38. *Philpottia* Meyrick, 1916: newly transferred to Plutellidae by synonymy with *Charixena* Meyrick, 1920.
39. *Picrodoxa* Meyrick, 1923: newly transferred to Epermeniidae. This genus has characters similar to those noted for *Agiton* and may in fact be relatively closely related.
40. *Piestoceros* Meyrick, 1907: newly transferred to Yponomeutidae. The genus conforms to characters of Yponomeutidae, notably such head characters as the labial palpi. The only known species, *Piestoceros*

- conjunctella* (Walker), also makes a rolled-leaf pupal case extended on a filament similar to that of *Urodus* species of the western hemisphere, although in *Urodus* the case is filigreed.
41. *Rhobonda* Walker, 1863: transferred to Choreutidae. This genus conforms to characters of Choreutidae and is related to *Melanoxena* Dognin.
 42. *Sesiomorpha* Snellen, 1885: transferred to Zygaenidae by Heppner (1981a). This genus is a junior synonym of *Burlacena* Walker, [1865], and is typical of tropical zygaenids.
 43. *Setiostoma* Felder and Rogenhofer, 1875: newly transferred to Glyphipterigidae. The only included species in the original description, *Setiostoma flaviceps* Felder and Rogenhofer, is clearly a member of the glyphipterigid genus *Ussara* Walker, 1864, precluding the use of *Setiostoma* Zeller, 1875 (described a few months after Felder and Rogenhofer) in the Stenomatinae (Oecophoridae).
 44. *Sezeris* Walker, 1863: transferred to Psychidae by virtue of synonymy with *Cebysa* Walker, 1854.
 45. *Spilogenes* Meyrick, 1938: transferred to Plutellidae by virtue of synonymy with *Ellabella* Busck, 1925.
 46. *Stichotactis* Meyrick, 1930: transferred to Plutellidae by virtue of synonymy with *Homadaula* Lower, 1899.
 47. *Symphorostola* Meyrick, 1927: transferred to Oecophoridae (Heppner, 1981a). Morphological characters, including the unusual genitalia and a scaled haustellum, conform to Xyloryctinae of Oecophoridae.
 48. *Thaumatotibia* Zacher, 1915: transferred to Tortricidae by Heppner, (1980). This long forgotten genus is a synonym of *Cryptophlebia* Walsingham, 1899, as far as can be determined from the original description of *Thaumatotibia*. The unique holotype has not been located.

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Catalog of Glyphipterigidae Auctorum Genera

The listing of each genus follows the sequence of genus name, author, date and page citation, and present family position, followed by the type-species and citation, mode of selection (subsequent designations show author, date, and citation), type locality, form of type (lectotypes have designator and year in parentheses, with citation), and present location of the type specimen. Below this data it is noted in which family the genus was originally described, when it was associated with the Glyphipterigidae auctorum (families are spelled as each author used them), and when and by whom it was first transferred to its present family position if in a family other than Glyphipterigidae. The original spellings are used: Meyrick and predecessors spelled Glyphipterigidae as Glyphipterygidae, since they used the emended spelling of *Glyphipteryx* Zeller, rather than the original *Glyphipterix* Hübner. Lectotypes indicated as by present designation have the actual designation data in the section on new lectotypes following the catalog.

Transfers of genera already published have no symbol by the family name at the right margin. New generic transfers are indicated by an asterisk (*) before the family name. Current generic names are in bold letters; synonyms or unavailable names are in italics. The currently accepted dates of various older works are used (see Nye 1975; Heppner 1982a).

Collections containing types are abbreviated as follows:

AMS	Australian Museum, Sydney, Australia
ANIC	Australian National Insect Collection, Canberra, Australia
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
BMNH	British Museum (Natural History), London, England
CAS	California Academy of Sciences, San Francisco, California, USA
DEI	Institut für Pflanzenschutzforschung Kleinmachnow, Eberswalde, DDR [formerly Deutsches Entomologisches Institut]
INHS	Illinois Natural History Survey, Urbana, Illinois, USA
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, USA
MNHP	Museum National d'Histoire Naturelle, Paris, France
NHNV	Naturhistorisches Museum, Vienna, Austria
RMNL	Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands
SAMA	South Australian Museum, Adelaide, Australia
SMF	Senckenburg Museum, Frankfurt, West Germany

SMS	Sarawak Museum, Kuching Sarawak, Malaysia
SMW	Staatliches Museum, Wiesbaden, West Germany
UMB	Übersee Museum, Bremen, West Germany
UMO	University Museum, Oxford, England
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
ZMC	Zoological Museum, Copenhagen, Denmark
ZMHB	Zoological Museum, Humboldt University, Berlin, DDR

Catalog of Genera Associated with Glyphipterigidae

Abrenthia Busck, 1915:87 Glyphipterigidae

Type-species: *Abrenthia cuprea* Busck, 1915:87, by monotypy. Type locality: USA: Roxboro, Pennsylvania [lectotype ♂ (present designation), USNM].

Originally described in Glyphipterygidae [sic].

Acrolepia Curtis, 1838:679 Acrolepiidae

Type-species: *Acrolepia autumnitella* Curtis, 1838:679 [= *Tortrix pygmeana* Haworth, [1811]:439], by original designation. Type locality (*autumnitella*): [England] [lectotype, BMNH?].

Originally described without family reference; subsequently transferred to Glyphipterygidae [sic] by Stainton (1854:169); transferred to Tineidae by Meyrick (1895:771); transferred to Acrolepiidae by Spuler (1910:453).

Actinoscelis Meyrick, 1912a:59 Heliodinidae

Type-species: *Actinoscelis irina* Meyrick, 1912a:59, by monotypy. Type locality: India: Bombay, Kanara [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Heliodinidae by Meyrick (1913b:19).

Adricara Walker, 1863:114 *Immidae

Type-species: *Adricara albidiscata* Walker, 1863:115, by monotypy. Type locality: Brazil, Ega, [=Tefé], Amazonas [holotype ♀, BMNH].

Originally described in Galleridae [=Pyralidae]; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:25), as a synonym of *Imma* Walker, [1859]; hereby transferred to Immidae as a junior subjective synonym of *Moca* Walker, 1863, new synonymy.

Aechmia Treitschke, 1833:69 Glyphipterigidae

Type-species: *Phalaena (Tortrix) fyeslella* [sic] Fabricius, 1798:493 [= *Phalaena (Tortrix) fueslella* Fabricius, 1781:301; = *Phalaena thrasonella* Scopoli, 1763:253], by subsequent designation of Westwood (1840:112). Type locality (*fueslella*): Germany: Kiel [lectotype ♂ (Diakonoff, 1977c:176), ZMC].

Originally described among the Tineina; subsequently transferred to Gly-

phipterygidae [sic] by Stainton (1854:173), as a synonym of *Glyphipteryx* [sic] auctorum [= *Glyphipterix* Hübner, 1825].

Aechmia sensu Zeller, 1847:881, included only *Tinagma metallicella* Duponchel, 1840, now in *Heliozela* Herrich-Schäffer, 1853 (Heliozelidae).

Aechmia sensu Stainton, 1854:176, included only *Aechmia dentella* Zeller, 1839, now in *Phaulernis* Meyrick, 1895 (Epermeniidae).

Aecimia [sic] Boisduval, 1836:138, misspelling Glyphipterigidae

A misspelling of *Aechmia* Treitschke, 1833, now a synonym of *Glyphipterix* Hübner, [1825].

Aeolocosma Meyrick, 1881:224 Oecophoridae

Type-species: *Aeolocosma iridozona* Meyrick, 1881:225, by subsequent designation of Meyrick (1922b:101). Type locality: Australia: Sydney, New South Wales [lectotype ♂ (Diakonoff, 1954:694), BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Oecophoridae (Oecophorinae) by Meyrick (1922b:101).

Agiton Turner, 1926a:145 *Epermeniidae

Type-species: *Agiton idioptila* Turner, 1926a:145, by monotypy. Type locality: Australia: [Lamington] National Park, Queensland [lectotype ♂ (present designation), ANIC].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Heliodinidae sensu Turner [=Yponomeutoidea] by Turner (1941:24); hereby transferred to Epermeniidae.

Alampla Diakonoff, 1978:36 Immidae

Type-species: *Imma palaeodes* Meyrick, 1914a:57, by original designation. Type locality: Taiwan: Shuisharyo [lectotype unselected, BMNH].

Originally described in Immidae.

Alicadra Walker, [1866]:1192 *Immidae

Type-species: *Alicadra vexatalis* Walker, [1866]:1192, by monotypy. Type locality: Brazil [holotype ♀, UMO].

Originally described in Herminidae [=Noctuidae]; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Imma* Walker, [1859], by Meyrick, (1913b:25); hereby transferred to Immidae as a junior subjective synonym of *Moca* Walker, 1863, **new synonymy**.

Allonomyia [sic] Ferguson, 1975:41, misspelling Choreutidae

A misspelling of *Allonyma* Busck, 1904, now a synonym of *Choreutis* Hübner, [1825].

Allonyma Busck, 1904:745 Choreutidae

Type-species: *Tortrix diana* Hübner, [1819–22]: pl. 44, fig. 274, by monotypy. Type locality: Europe [type lost?].

Originally described in Yponomeutidae; subsequently transferred to Gly-

phipterygidae [sic] by Meyrick (1913b:34); transferred to Choreutidae as a junior subjective synonym of *Eutromula* Frölich, 1828, by Bradley (1972:12); now a junior subjective synonym of *Choreutis* Hübner, [1825] (Heppner, 1981a:53).

Allonyma [sic] Fracker, 1915:77, misspelling Choreutidae

A misspelling of *Allononyma* Busck, 1904, now a synonym of *Choreutis* Hübner, [1825].

Allotrophia Diakonoff, 1954:688 *Oecophoridae

Type-species: *Orosana percussana* Walker, 1864:998, by original designation. Type locality: Australia: Tasmania [holotype ♂, BMNH].

Originally described in Hypertrophinae of Glyphipterygidae [sic]; hereby transferred to Oecophoridae: Hypertrophinae.

Amphiclada Meyrick, 1912a:60 Heliodinidae

Type-species: *Amphiclada fervescens* Meyrick, 1912a:60, by monotypy. Type locality: Grenada: St. George's [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Heliodinidae by Meyrick (1913b:18).

Amphimelas Turner, 1929:306 Oecophoridae

Type-species: *Amphimelas argopasta* Turner, 1929:307 [= *Chereuta tinthalea* Meyrick, 1906a:33], by monotypy. Type locality (*argopasta*): Australia: New South Wales [lectotype unselected, ANIC?].

Originally described in Glyphipterygidae [sic]; *Amphimelas* Turner, 1929, is now a junior subjective synonym of *Chereuta* Meyrick, 1906, in Oecophoridae: Xyloryctinae.

Anacampsoides Bruand, 1850b:32 Glyphipterigidae

Type-species: *Heribeia simplicella* Stephens, 1834:263, by monotypy. Type locality: England [lectotype ♂ (Diakonoff, 1977c:174), BMNH].

Originally listed in a catalog under Tineidae; subsequently a nomen oblitum and a junior subjective synonym of *Glyphipterix* Hübner, [1825], in Glyphipterigidae.

Anthophila Haworth, [1811]:471 Choreutidae

Type-species: *Anthophila fabricii* Haworth, [1811]:471, emendation [= *Phalaena* (*Tortrix*) *fabriciana* Linnaeus, 1767:880], by subsequent designation of Fletcher (1929:16). Type locality (*fabriciana*): Europe [type, Linnean Society?, London].

Originally described without family placement; subsequently transferred to Choreutidae by Stainton (1859:158), as a synonym of *Simaethis* Leach, 1815; now considered a valid genus in Choreutidae.

There has been some reference in the literature to a homonym of *Anthophila* Haworth, other than *Anthophila* Ochsenheimer, but this refers to the genus *Anthophilus* in Hymenoptera which is spelled differently.

Anthophila Ochsenheimer, 1816:93 Noctuidae

Type-species: *Noctua purpurina* [Denis and Schiffermüller], 1775:88, by subsequent designation of Duponchel (1829:72). Type locality: Austria: Vienna [type lost?].

Preoccupied by *Anthophila* Haworth, [1811] (Choreutidae); currently considered to be a junior objective synonym of *Porphyrinia* Hübner, [1821], in Noctuidae.

Anthophilae Hübner, [1806]:[2] Noctuidae

Rejected for nomenclatural purposes by Opinion 97 (ICZN, 1926). *Noctua purpurina* [Denis and Schiffermüller], 1775:88, was the only included species, now in *Porphyrinia* Hübner, [1821] (Noctuidae).

Anthrophila [sic] Treitschke, 1832:134 Noctuidae

A misspelling of *Anthophila* Ochsenheimer, 1816 [not *Anthophila* Haworth, 1811], now a synonym of *Porphyrinia* Hübner, [1821], in Noctuidae.

Antispastis Meyrick, 1926b:307 *Acrolepiidae

Type-species: *Antispastis xylophragma* Meyrick, 1926b:307, by monotypy. Type locality: Peru: Cocapata [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic]; hereby transferred to Acrolepiidae.

Antophila Hübner, [1806]:[2] Noctuidae

An original multiple spelling of *Anthophilae* Hübner, [1806]:[2], published in a work rejected for nomenclatural purposes by Opinion 97 (ICZN, 1926); now a synonym (although unavailable) of *Porphyrinia* Hübner, [1821], in Noctuidae.

Anthophila [sic] Bleszynski, Razowski, and Zukowski, 1965:413 Choreutidae

A misspelling of *Anthophila* Haworth, [1811] [not *Anthophila* Ochsenheimer, 1816], now in Choreutidae.

Antophyla [sic] Duponchel, 1829:72 Noctuidae

A misspelling of *Anthophila* Ochsenheimer, 1816 [not *Anthophila* Haworth, 1811], now synonym of *Porphyrinia* Hübner, [1821], in Noctuidae.

Apistomorpha Meyrick, 1881:247 Glyphipterigidae

Type-species: *Apistomorpha argyrosema* Meyrick, 1881:247 by monotypy. Type locality: Australia: New South Wales [lectotype unselected, BMNH].

Originally described in Glyphipterygidae [sic]; considered a junior subjective synonym of *Glyphipterix* Hübner, [1825], by Meyrick (1913b:41); here considered a distinct genus.

Aprata Moore, 1883:106 Psychidae

Type-species: *Aprata mackwoodii* Moore, 1883:106, by subsequent des-

ignation of Walsingham and Durrant, 1900b:582. Type locality: Ceylon [= Sri Lanka] [holotype ♂, BMNH].

Originally described in Psychidae; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:32); hereby returned to Psychidae.

Aproopta Turner, 1919:171

Oecophoridae

Type-species: *Aproopta melanchlaena* Turner, 1919:172, by monotypy. Type locality: Australia: Katoomba, New South Wales [holotype ♂, AMS].

Originally described in Gelechiinae [=Gelechiidae]; subsequently included in Glyphipterygidae [sic] by Fletcher (1929:20); transferred to Stenomitidae by Sattler (1973:171); now in Oecophoridae: Stenomatinae.

Araeolepia Walsingham, 1881:303

Plutellidae

Type-species: *Araeolepia subfasciella* Walsingham, 1881:303, by monotypy. Type locality: USA: Currant Creek, Grant Co., Oregon [lectotype ♂ (present designation), BMNH].

Originally described in Tineidae; subsequently transferred to Glyphipterygidae [sic] by Busck (1925:46); transferred to Plutellidae by Heppner (1978a:51).

Archimaga Meyrick, 1905:609

Tortricidae

Type-species: *Archimaga pyractis* Meyrick, 1905:609, by monotypy. Type locality: Ceylon [=Sri Lanka]: Maskeliya [lectotype ♂ (Clarke, 1963:71), BMNH].

Originally described in Plutellidae and noted to be "allied to *Hilarographa*"; subsequently transferred to Chlidanotidae by Meyrick (1906b:411), now a subfamily of Tortricidae.

Ardrupia [sic] Busck, 1911:228

Copromorphidae

One of two original spellings of *Ordrupia* Busck, 1911, corrected by Busck (1912:8); now in Copromorphidae.

Asterivora Dugdale, 1979:461

Choreutidae

Type-species: *Simaethis combinatana* Walker, 1863:456, by original designation. Type locality: New Zealand [lectotype unselected, BMNH].

Originally described in Choreutidae.

Asterophaga Horning and Greenwood, 1977:295

Choreutidae

A nomen nudum without family reference; now a synonym of *Asterivora* Dugdale, 1979, in Choreutidae.

Atichia [sic] Ochsenheimer, 1808:11

Zygaenidae

A misspelling of *Atychia* Ochsenheimer, 1808:10, now a synonym of *Adscita* Retzius, 1783, in Zygaenidae.

Atractoceros Meyrick, 1936a:40

Brachodidae

Type-species: *Phycodes xanthoprocta* Meyrick, 1914c:283, by original

designation. Type locality: Nyasaland [=Malawi]: Mt. Mlanje [lectotype unselected, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Brachodidae by Heppner (1979a:127).

Atychia Ochseneheimer, 1808:10

Zygaenidae

Type-species: *Sphinx statice* Linnaeus, 1758:495, by subsequent designation of Tremewan (1973:119). Type locality: Europe [type, Linnean Society, London].

Originally described in Sphingidae; currently a junior synonym of *Adscita* Retzius, 1783, in Zygaenidae.

Atychia Latreille, 1809:214

Brachodidae

Type-species: *Sphinx chimaera* Hübner, 1796:pl. 1, fig. 1 [= *Sphinx appendiculata* Esper, 1783:227], by subsequent designation of Latreille (1810:441). Type locality (*chimaera*): Europe [type lost?]; (*appendiculata*): Europe [lectotype ♀ (present designation), SMW].

Originally described without family placement; subsequently transferred to Atychidae by Duponchel (1835:169); transferred to Tineidae by Staudinger (1870:229); transferred to Plutellidae by Meyrick (1906c:169); transferred to Glyphipterygidae [sic] by Meyrick (1913b:29); transferred to Brachodidae (formerly Atychiidae) by Heppner (1979a:127), as a junior subjective synonym of *Brachodes* Guenée, 1845.

Atychia Latreille, 1809, is a junior homonym of *Atychia* Ochseneheimer, 1808 (Zygaenidae).

Badera Walker, 1866:1819

Choreutidae

Type-species: *Badera pretiosa* Walker, 1866:1819, by subsequent designation of Meyrick (1914d:18). Type locality: [Indonesia]: Java [lectotype ♂ (present designation), BMNH].

Originally described in Tineidae; subsequently transferred to Plutellidae by Meyrick (1907:97); transferred to Glyphipterygidae [sic] Meyrick (1913b:33) as a synonym of *Tortyra* Walker, 1863; transferred to Choreutidae as a junior subjective synonym of *Saptha* Walker, 1864, by Heppner (1981a:55).

Birrhana Walker, [1865]:145

*Immididae

Type-species: *Birrhana consocia* Walker, [1865]:145, by monotypy. Type locality: India: Mysol [holotype ♂, UMO].

Originally described in Melameridae [=Noctuidae]; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Imma* Walker, [1859], by Meyrick (1913b:25); hereby transferred to Immididae as a distinct genus.

Brachodes Guenée, 1845:311

Brachodidae

Type-species: *Brachodes vernetella* Guenée, 1845:311 [= *Chimera* [sic]

funebis Feisthamel, 1833:259], by monotypy. Type locality (*vernetella*): Persia [type, MNHP?].

Originally described in a catalog under Tineae; subsequently transferred to Plutellidae by Meyrick (1906c:169); transferred to Glyphipterygidae [sic] as a synonym of *Atychia* Latreille, 1809, by Meyrick (1913b:29), and as a distinct genus in Brachodinae by Agenjo (1966:[148]); transferred to Brachodidae by Heppner (1979a:127).

Bradyptesis Sodoffsky, 1837:83

Zygaenidae

An unjustified replacement name for *Atychia* Ochsenheimer, 1808 [not *Atychia* Latreille, 1809], now a junior objective synonym of *Adscita* Retzius, 1783, in Zygaenidae.

Bradyptesis sensu Kasy, 1979:5

Brachodidae

An incorrect use of *Bradyptesis* as a replacement name for *Atychia* Latreille, 1809, now in Brachodidae as a junior synonym of *Brachodes* Guenée.

Brenthia Clemens, 1860:172

Choreutidae

Type-species: *Brenthia pavonacella* Clemens, 1860:172, by monotypy. Type locality: USA: [Pennsylvania] [holotype ♀, ANSP].

Originally described in Tineina; subsequently transferred to Choreutina by Zeller (1875:323); transferred to Plutellidae by Meyrick (1907:108); transferred to Choreutidae by Heppner (1977b:633).

Bryonympha Meyrick, 1930a:560

*Immidae

Type-species: *Bryonympha silvana* Meyrick, 1930a:560, by monotypy. Type locality: Comoro Is.: Grand Comoro Id. [holotype ♀, BMNH].

Originally described in Xyloryctidae; subsequently transferred to Glyphipterygidae [sic] by Viette (1954:13); hereby transferred to Immidae.

Burlacena Walker, [1865]:80

Zygaenidae

Type-species: *Burlacena aegerioides* Walker, [1865]:80, by subsequent designation of Meyrick (1914d:7). Type locality: New Guinea [holotype ♂, BMNH].

Originally described in Zygenidae [sic]; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:25); transferred to Yponomeutidae by Common (1970b:813); hereby returned to Zygaenidae.

Bursadella Snellen, 1880:83

*Immidae

Type-species: *Bursadella dichroalis* Snellen, 1880:83, by subsequent designation of Meyrick (1906c:170). Type locality: [Indonesia]: Silago, Sumatra [holotype ♂, RMNL].

Originally described in Tineina; subsequently transferred as a synonym of *Imma* Walker, [1859], in Plutellidae by Meyrick (1906c:170), and in Glyphipterygidae [sic] by Meyrick (1913b:25); hereby transferred to Immidae as a distinct genus.

Calantica Zeller, 1847:811

Yponomeutidae

Type-species: *Calantica albella* Zeller, 1847:811 [= *Calantica dealbatella* Zeller, 1847:811], by subsequent designation of Friese (1960:38). Type locality (*albella*): Germany: Taunus [type?].

Originally described in Tineides; subsequently transferred to Hyponomeutidae [sic] by Heinemann (1870:101); transferred to Hemerophilidae by Walsingham (1914:319); transferred to Yponomeutidae as a junior synonym of *Niphonympha* Meyrick, 1914, by Friese (1960:38).

Calantica Zeller, 1847, is a junior homonym of *Calantica* Gray, 1825 (Crustacea).

Callartona Hampson, [1893]:233

*Immidiae

Type-species: *Callartona purpurascens* Hampson, [1893]:233, by original designation. Type locality: India: Nilgiris [holotype ♀, BMNH].

Originally described in Zygaenidae; subsequently transferred as a synonym of *Imma* Walker, [1859], to Plutellidae by Meyrick (1906c:170), and to Glyphipterygidae [sic] by Meyrick (1913b:25); hereby transferred to Immidae as a junior subjective synonym of *Moca* Walker, 1863, **new synonymy**.

Callisto Stephens, 1834:276

Gracillariidae

Type-species: *Gracillaria guttea* Haworth, 1828:531 [= *Tinea denticulella* Thunberg, 1794:97], by subsequent designation of Bradley (1966a:131). Type locality (*guttea*): England [lectotype ♂ (Bradley, 1966a:131), UMO].

Originally described in Yponomeutidae; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Glyphipteryx* [sic] Hübner, [1825], by Stainton (1854:173); now a distinct genus in Gracillariidae.

Callatolmis Butler, 1877:348

Brachodidae

Type-species: *Lycomorpha coleoprata* Walker, 1854:288, by original designation. Type locality: Brazil: Tapayos [holotype ♂, BMNH].

Originally described in Lithosiidae [=Arctiidae]; subsequently transferred to Glyphipterygidae [sic] as a junior synonym of *Sagalassa* Walker, 1856, by Meyrick (1913b:31); transferred to Brachodidae as a distinct genus by Heppner (1979a:127).

Callizyga Turner, 1894:132

Oecophoridae

Type-species: *Callizyga dispar* Turner, 1894:132, by monotypy. Type locality: Australia: Brisbane, Queensland [lectotype ♂ (present designation), ANIC].

Originally described in Oecophoridae; subsequently transferred to Hyponomeutinae [sic] in Plutellidae together with *Imma* Walker, [1859], by Turner (1913:208); transferred to Oecophoridae by Meyrick (1922b:137); now in Oecophoridae: Depressariinae (Amphisbatini).

Caloreas Heppner, 1977b:631

Choreutidae

Type-species: *Choreutis apocynoglossa* Heppner, 1976:256, by original

designation. Type locality: USA: Del Valle Lake, Alameda Co., California [holotype ♂, CAS].

Originally described in Choreutidae.

Carmentina Meyrick, 1930b:597

Glyphipterigidae

Type-species: *Carmentina iridesma* Meyrick, 1930b:598, by monotypy.

Type locality: Solomon Is.: Bougainville [holotype ♀, BMNH].

Originally described in Yponomeutidae; subsequently transferred to Glyphipterigidae as the senior subjective synonym of *Metapodistis* Meyrick, 1933, by Heppner (1982c).

Carna Walker, 1864:1038

Gelechiidae

Type-species: *Rhobonda punctatella* Walker, 1864:802, by monotypy of *Rhobonda*. Type locality: Brazil: Ega [=Tefé], Amazonas [holotype ♀, BMNH].

Originally described in Gelechidae [sic] as a replacement name for *Rhobonda* Walker, 1864, a junior homonym of *Rhobonda* Walker, 1863, in Choreutidae. *Carna* Walker, 1864, is a junior homonym of *Carna* Gistel, 1848 (Echinodermata), and is currently considered to be a junior synonym of *Dichomeris* Hübner, [1825], in Gelechiidae: *Dichomerinae*.

Cebysa Walker, 1854:486

Psychidae

Type-species: *Cebysa leucotelus* Walker, 1854:486, by monotypy. Type locality: Australia: Sydney, New South Wales [holotype ♀, BMNH].

Originally described in Lithosiidae [=Arctiidae]; subsequently transferred to Plutellidae by Meyrick (1907:92); transferred to Glyphipterygidae [sic] by Meyrick (1913b:32); transferred to Psychidae by Common (1970b:804).

Cercosimma Diakonoff, 1948:197

*Immidae?

Type-species: *Cercosimma electrodes* Diakonoff, 1948:199, by original designation. Type locality: Indonesia: Buru Id. [holotype ♂, RMNL?].

Originally described in Glyphipterygidae [sic]; hereby tentatively transferred to Immidae.

Chalenata Walker, 1864:1001

Noctuidae

Type-species: *Chalenata micaceella* Walker, 1864:1001, by monotypy. Type locality: Brazil, Ega [=Tefé], Amazonas [holotype ♀, BMNH].

Originally described in Choreutidae; now in Noctuidae: Acontiinae.

Charitographa Diakonoff, 1979:291

Tortricidae

Type-species: *Hilarographa mikadonis* Stringer, 1930:418, by original designation. Type locality: Japan: Sapporo [holotype ♂, BMNH].

Originally described in the tribe Hilarographini of Tortricidae: Chlidanotinae.

Charixena Meyrick, 1920a:279

*Plutellidae

Type-species: *Philpottia iridoxa* Meyrick, 1916:417, by original designa-

tion. Type locality: New Zealand: Mt. Burns, Hunter Mts., South Island [lectotype unselected, BMNH].

Originally described as a replacement name for *Philpottia* Meyrick, 1916, in Glyphipterygidae [sic]; hereby transferred to Plutellidae.

Charixena Meyrick, 1921b:335, is a redescription of *Charixena* Meyrick, 1920.

Charizena [sic] Neave, 1939:673

*Plutellidae

A misspelling of *Charixena* Meyrick, 1920, hereby in Plutellidae.

Chimaera Ochsenheimer, 1808:2

Brachodidae

Type-species: *Sphinx chimaera* Hübner, 1796:pl. 1, fig. 1 [= *Sphinx appendiculata* Esper, 1783:227], by subsequent designation of Blanchard (1840:474). Type locality (*chimaera*): Europe [type lost?]. Preoccupied by *Chimaera* Linnaeus, 1758 (Pisces).

Originally described in Sphinges; subsequently transferred to Chimerites by Blanchard (1840:474); transferred to Glyphipterygidae [sic] as a junior synonym of *Phycodes* Guenée, 1852, by Meyrick (1913b:32); transferred to Brachodidae as a junior synonym of *Brachodes* Guenée, 1845, by Heppner (1979a:127).

Walsingham (1900b:568) designated *Chimaera radiata* Ochsenheimer, 1808:5, as the type-species of *Chimaera* Ochsenheimer, thus, making the genus a synonym of *Phycodes* Guenée, 1852, due to homonymy with *Chimaera* Linnaeus, 1758, and equal type-species. However, the type-species of *Chimaera* Ochsenheimer, 1808, is *Sphinx chimaera* Hübner, 1796, by an earlier designation (Blanchard, 1840), thus making the genus a junior synonym of *Brachodes* Guenée, 1845.

Chimera [sic] Feisthamel, 1833:259

Brachodidae

A misspelling of *Chimaera* Ochsenheimer, 1808, now a junior synonym of *Brachodes* Guenée, 1845, in Brachodidae.

Chloreutis [sic] Viette, 1948a: 40

Choreutidae

A misspelling of *Choreutis* Hübner, [1825], in Choreutidae.

Chordates Snellen, 1877:49

Choreutidae

Type-species: *Simaethis pronubana* Snellen, 1877:48, by subsequent designation of Fletcher (1929:47). Type locality: [Indonesia]: Java [lectotype ♀ (present designation), RMNL].

Originally described in Tineina; subsequently transferred to Hemerophilidae as a junior synonym of *Tortyra* Walker, 1863, by Walsingham (1914:312); transferred to Choreutidae as a junior subjective synonym of *Saptha* Walker, 1864, by Heppner (1981a:55).

Choredates [sic] Pagenstecher, 1884:289

Choreutidae

A misspelling of *Chordates* Snellen, 1877, now a synonym of *Saptha* Walker, 1864, in Choreutidae.

Choregia Felder and Rogenhofer, 1875:6 Choreutidae

Type-species: *Choregia fulgens* Felder and Rogenhofer, 1875:6, by subsequent designation of Heppner (1981a:56). Type locality: Colombia: Bogota [lectotype ♂ (present designation), BMNH].

Originally described in Tineidae; subsequently transferred to Choreutiden by Zeller (1877:191) as *Choregia* Zeller; transferred to Hemerophilidae as a junior synonym of *Tortyra* Walker, 1863, by Walsingham (1914:312); transferred to Choreutidae as a junior subjective synonym of *Tortyra* Walker, 1863, by Heppner (1981a:56).

Felder and Rogenhofer (1875) attributed *Choregia* to Zeller but the Zeller description did not appear until 1877.

Choregia Zeller, 1877:191 Choreutidae

Type-species: *Choregia fulgens* Felder and Rogenhofer, 1875:6, by subsequent designation of Meyrick (1914d:18). Type locality: Colombia: Bogota [lectotype ♂ (present designation), BMNH]. Preoccupied by *Choregia* Felder and Rogenhofer, 1875 (Choreutidae).

Originally described in Choreutiden; subsequently transferred to Hemerophilidae as a junior synonym of *Tortyra* Walker, 1863, by Walsingham (1914:312); transferred to Choreutidae as a junior subjective synonym of *Tortyra* Walker, 1863, by Heppner (1981a:56).

Chorentes [sic] Morris, 1871:iv Choreutidae

A misspelling of *Choreutis* Hübner, [1825], now in Choreutidae.

Chorentis [sic] Turner, 1898:203 Choreutidae

A misspelling of *Choreutis* Hübner, [1825], now in Choreutidae.

Choreutes Treitschke, 1835:31 Choreutidae

An unjustified emendation of *Choreutis* Hübner, [1825], now in Choreutidae.

Choreutes Burmeister, 1838 (Collembola), is a junior homonym of *Choreutes* Treitschke, 1835.

Choreuthis [sic] Hackman, 1947:71 Choreutidae

A misspelling of *Choreutis* Hübner, [1825], now in Choreutidae.

Choreutidia Sauber, 1902:702 Choreutidae

Type-species: *Choreutidia sexfasciella* Sauber, 1902:702, by monotypy. Type locality: Philippines: Luzon [holotype ♂, SMF].

Originally described in Hyponomeutidae [sic]; subsequently transferred to Glyphipterygidae [sic] as a junior synonym of *Choreutis* Hübner, [1825], by Meyrick (1913b:38); transferred to Choreutidae as a junior subjective synonym of *Choreutis* Hübner, [1825], by Heppner (1981a:53).

Choreutis Hübner, [1825]:373 Choreutidae

Type-species: [*Phalaena*] *pariana* Clerck, 1759:pl. 10, fig. 9, by subse-

quent designation of Walsingham (1908:987). Type locality: Europe [type lost?].

Originally described in Tortrices; subsequently transferred (as *Choreutes* [sic]) to Choreutidae by Stainton (1859:158); transferred to Glyphipterygidae [sic] by Wocke (1871:265); now in Choreutidae.

Choreutis of authors [not Hübner, 1825] Choreutidae

This name was used by most authors in reference to *Pylalis myllerana* Fabricius, 1794, and congeners, especially since Meyrick (1914d), but the first valid type-species designation for *Choreutis* Hübner, [1825], was only recently confirmed to be that of Walsingham (1908:987), being *Phalaena pariana* Clerck, 1759, and not *Pylalis myllerana* Fabricius, 1794. Consequently, the name *Choreutis* Hübner, [1825], has been transferred to species until recently referred to *Eutromula* Frölich, 1828, while *Choreutis* of authors has been given the new name *Prochoreutis* Diakonoff and Heppner, 1980 (Diakonoff and Heppner, 1980:196).

Chrysocentris Meyrick, 1914c:284 Glyphipterigidae

Type-species: *Chrysocentris clavaria* Meyrick, 1914c:284, by monotypy. Type locality: Nyasaland [=Malawi]: Mt. Mlanje [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic].

Cibdeloses Durrant, 1919:121 Zygaenidae

Type-species: *Cibdeloses dolopis* Durrant, 1919:121, by original designation. Type locality: India: Khasis, Assam [holotype ♀, BMNH].

Originally described in Hemerophilidae [=Choreutidae]; subsequently transferred to Zygaenidae by Heppner (1981a:15).

Circica Meyrick, 1888:88 Glyphipterigidae

Type-species: *Circica cionophora* Meyrick, 1888:88, by monotypy. Type locality: New Zealand: Christchurch, South Island [lectotype ♂ (present designation), BMNH].

Originally described in Tineina; subsequently transferred to Glyphipterygidae [sic] as a junior synonym of *Glyphipteryx* [sic] Hübner, [1825], by Meyrick (1913b:41); now considered as a distinct genus in Glyphipterigidae.

Cloreatis [sic] Kautz, 1930:28 Choreutidae

A misspelling of *Choreutis* Hübner, [1825], in Choreutidae.

Colpotorna Meyrick, 1920b:325 *Psychidae

Type-species: *Colpotorna lasiopa* Meyrick, 1920b:326, by monotypy. Type locality: Australia: Brisbane, Queensland [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic]; hereby transferred to Psychidae.

Coridomorpha Meyrick, 1914b:111 *Oecophoridae

Type-species: *Coridomorpha stella* Meyrick, 1914b:111, by monotypy.

Type locality: New Zealand [lectotype unselected, BMNH].

Originally described in Glyphipterygidae [sic]; hereby transferred to Oecophoridae: Oecophorinae.

Corsocasis Meyrick, 1912a:59

Heliodinidae

Type-species: *Corsocasis coronias* Meyrick, 1912a:59, by monotypy. Type locality: India and Sri Lanka [lectotype unselected, BMNH?].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Heliodinidae by Meyrick (1913b:20).

Cotaena Walker, [1865]:21

Glyphipterigidae

Type-species: *Cotaena mediana* Walker, [1865]:21, by monotypy. Type locality: Brazil: Para [holotype ♀, UMO].

Originally described in Aegeriidae [=Sesiidae]; subsequently transferred to Heliodinidae by Naumann (1971:15); transferred to Glyphipterigidae by Heppner (1981a:44).

Cronicombra Meyrick, 1920b:327

Glyphipterigidae

Type-species: *Cronicombra granulata* Meyrick, 1920b:327, by monotypy. Type locality: Brazil: Para [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic].

Cylicophora Turner, 1927:156

Yponomeutidae

Type-species: *Cylicophora collina* Turner, 1927:156, by monotypy. Type locality: Australia: Cradle Mt., Tasmania [holotype ♂, ANIC].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Yponomeutidae as a junior subjective synonym of *Tanaoctena* Turner, 1913, by Clarke (1971:167).

Davendra Moore, 1887:520

*Immidae

Type-species: *Davendra mackwoodii* Moore, 1887:520, by original designation. Type locality: Ceylon [=Sri Lanka] [lectotype unselected, BMNH].

Originally described in Gelechiidae; subsequently transferred to Plutellidae as a junior synonym of *Imma* Walker, [1859], by Meyrick (1906c:170); hereby transferred to Immidae as a junior subjective synonym of *Imma* Walker, [1859].

Desmidoloma Erschoff, 1892:671

Glyphipterigidae

Type-species: *Staintonia fulgens* Erschoff, 1877:347 [= *Argyresthia perornatella* Walker, 1864:840], by monotypy. Type locality (*fulgens*): China: Amur region, [Manchuria] [holotype ♀, lost?].

Originally described without family reference; subsequently transferred to Glyphipterygidae [sic] as a junior subjective synonym of *Glyphipteryx* [sic] Hübner, [1825], by Meyrick (1913b:41); here considered a junior subjective synonym of *Lepidotarphius* Pryer, 1877, in Glyphipterigidae.

Diploschizia Heppner, 1981b:311 Glyphipterigidae

Type-species: *Glyphipteryx* [sic] *impigritella* Clemens, 1863:9, by original designation. Type locality: USA: [Easton, Northampton County, Pennsylvania] [holotype ♂, ANSP].

Originally described in Glyphipterigidae.

Ditrigonophora Walsingham, 1897b:117 *Yponomeutidae?

Type-species: *Ditrigonophora marmoreipennis* Walsingham, 1897b:118, by original designation. Type locality: Grenada: Balthazar [lectotype (present designation), BMNH].

Originally described in Glyphipteryginae [sic] of Hyponomeutidae [sic]; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:40); hereby tentatively transferred to Yponomeutidae, [syntypes lack abdomens and heads].

Douglasia Stainton, 1854:179 Douglesiidae

Type-species: *Gracilaria* [sic] *ocnerostomellum* Stainton, 1850:6, by original designation and monotypy. Type locality: England [lectotype unselected, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Elachistidae by Meyrick (1895:684); transferred to Douglesiidae [sic] by Meyrick (1928:721); now considered a junior subjective synonym of *Tinagma* Zeller, 1839, in Douglesiidae.

Dudua Walker, 1864:1000 Tortricidae

Type-species: *Dudua hesperialis* Walker, 1864:1000, by monotypy. Type locality: Sarawak [holotype ♂, BMNH].

Originally described in Choreutidae; subsequently transferred to Tortricidae by Walsingham (1900a:135).

Electrographa Meyrick, 1912a:63 Glyphipterigidae

Type-species: *Electrographa thiolychna* Meyrick, 1912a:63, by monotypy. Type locality: Burma: Momeit [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic].

Ellabella Busck, 1925:46 Plutellidae

Type-species: *Ellabella editha* Busck, 1925:46, by original designation. Type locality: Canada: Saanichton, British Columbia [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Plutellidae by Heppner (1978a:50).

Embolostoma Diakonoff, 1977b:51 Tortricidae

Type-species: *Embolostoma plutostola* Diakonoff, 1977b:52, by original designation. Type locality: Indonesia: West Java [holotype ♀, RMNL].

Originally described in the tribe Hilarographini of Tortricidae: Chlidanotinae.

Embryonopsis Eaton, 1876:61

Yponomeutidae

Type-species: *Embryonopsis halticella* Eaton, 1876:61, by monotypy.
Type locality: New Zealand: Heard Id. [lectotype ♂ (Common, 1970a:231), BMNH].

Originally described in Gelechiidae; subsequently transferred to Yponomeutidae by Viette (1948b:16).

Encratora Meyrick, 1923:618

*Heliodinidae

Type-species: *Encratora plumbigera* Meyrick, 1923:618, by monotypy.
Type locality: India: Shillong, Assam [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic]; hereby transferred to Heliodinidae.

Entomoloma Ragonot, 1875:45

Choreutidae

Type-species: *Tortrix nemorana* Hübner, [1796–99]:pl. 1, fig. 3, by subsequent designation of Walsingham (1908:988). Type locality: Europe [type lost?].

Originally described in Choreutina [=Choreutidae]; subsequently transferred to Glyphipterygidae [sic] as a junior synonym of *Simaethis* Leach, 1815, by Meyrick (1913b:34); transferred to Choreutidae as a junior subjective synonym of *Eutromula* Leach, 1815, by Arita and Diakonoff (1979:8); now a junior subjective synonym of *Choreutis* Hübner, [1825] (Heppner, 1981a:53).

Epicroesa Meyrick, 1907:94

*Heliodinidae

Type-species: *Epicroesa ambrosia* Meyrick, 1907:96, by subsequent designation of Meyrick (1914d:17). Type locality: Australia: Queensland [lectotype unselected, BMNH].

Originally described in Plutellidae; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1912a:58); hereby transferred to Heliodinidae.

Epithetica Turner, 1923:165

*Oecophoridae

Type-species: *Epithetica typhoscia* Turner, 1923:165, by monotypy. Type locality: Australia: Lismore, New South Wales [lectotype ♂ (present designation), ANIC].

Originally described in Glyphipterygidae [sic]; hereby transferred to Oecophoridae: Hypertrophinae.

Ereunetis Meyrick, 1881:258

Tineidae

Type-species: *Ereunetis iuloptera* Meyrick, 1881:260, by subsequent designation of Walsingham (1907:714). Type locality: Australia: Sydney, New South Wales [lectotype unselected, BMNH].

Originally described in Erechthiidae [sic] [= Tineidae]; subsequently transferred to Lyonetiidae [sic]; now considered in Tineidae.

Meyrick (1912b:122) listed a new species of *Ereunetis* under Glyphipterygidae [sic] but the genus has always been associated with the Tineoidea and is now in Tineidae.

Ernolytis Meyrick, 1922a:488 Glyphipterigidae

Type-species: *Ernolytis chlorospora* Meyrick, 1922a:488, by monotypy.

Type locality: Fiji: Lolotu [lectotype unselected, BMNH].

Originally described in Glyphipterygidae [sic].

Euprophantis Meyrick, 1921a:191 Gracillariidae

Type-species: *Euprophantis autoglypta* Meyrick, 1921a:191, by monotypy. Type locality: [Indonesia]: Pekalongan, Java [lectotype ♂ (present designation), RMNL].

Originally described in Gracilariidae [sic]; subsequently partially associated with *Glyphipterix* Hübner, [1825]; now in Gracillariidae.

Eupselia Meyrick, 1881:216 Oecophoridae

Type-species: *Eupselia satrapella* Meyrick, 1881:220, by subsequent designation of Meyrick (1922b:148). Type locality: Australia: Sydney, New South Wales [lectotype unselected, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Oecophoridae (Oecophorinae) by Meyrick (1922b:148).

Euthorybeta Turner, 1913:200 Brachodidae

Type-species: *Euthorybeta xanthoplaca* Turner, 1913:201, by original designation. Type locality: Australia: Stadbroke Id., Queensland [holotype ♀, ANIC].

Originally described in Plutellidae (Yponomeutinae); subsequently transferred to Brachodidae by Heppner (1979a:127).

Eutromula Frölich, 1828:11 Choreutidae

Type-species: [*Phalaena*] *pariana* Clerck, 1759:pl. 10, fig. 9, by subsequent designation of Fletcher (1929:93). Type locality: Europe [type lost?].

Originally described without family placement; subsequently transferred to Glyphipterygidae [sic] by Fletcher (1929:93) as a junior synonym of *Anthophila* Haworth, [1811]; transferred to Choreutidae by Heppner (1977b:633); now a junior objective synonym of *Choreutis* Hübner, [1825] (Heppner, 1981a:53).

Ganabalia Diakonoff, 1975:316 Tortricidae

Type-species: *Ganabalia planipes* Diakonoff, 1975:317, by original designation. Type locality: Indonesia: Celebes [holotype ♂, BMNH].

Originally described in "Choreutinae" of Tortricidae; transferred to Tortricidae: Olethreutinae by Diakonoff (1981:71).

Gauris Hübner, 1821:[1] Choreutidae

Type-species: *Phalaena* (*Tortrix*) *albertiana* Cramer, 1781:163, by monotypy. Type locality: Surinam [type lost?].

Originally listed in an index and described in Tineina by Hübner ([1825]:374); subsequently transferred to Atychianae [sic] of Tineidae by Walsingham (1892:529); transferred to Glyphipteryginae [sic] of Hypono-

meutidae [sic] by Walsingham (1897b:120); transferred to Choreutidae as a junior objective synonym of *Hemerophila* Hübner, [1817], by Heppner (1977b:634).

Glyphipterix Hübner, [1825]:421

Glyphipterigidae

Type-species: *Glyphipterix linneella* Hübner, [1825]:421 [= *Tortrix linneana* Hübner, [1796–99]:pl. 14, fig. 8; = *Tinea bergstraesserella* Fabricius, 1781:302] [not *Phalaena linneella* Clerck, 1759:pl. 12, fig. 8 (Agonoxenidae)], by subsequent designation of Duponchel (1845:243). Type locality (*linneella* Hübner): Europe [type lost?].

Originally described in Tineae; subsequently transferred to Glyphipterygidae [sic] by Stainton (1854:173).

Glyphipterys [sic] Christoph, 1882:38

Glyphipterigidae

A misspelling of *Glyphipterix* Hübner, [1825], now in Glyphipterigidae.

Glyphipteryx Curtis, 1827:152

Agonoxenidae

Type-species: [*Phalaena*] *linneella* Clerck, 1759:pl. 12, fig. 8, by original designation. Type locality: Europe [type lost?].

Originally described without family placement; subsequently a nomen oblitum until resurrected and transferred to Momphidae (Cosmopteriginae) by Bradley (1972:25); here considered a junior objective synonym of *Chrysoclista* Stainton, 1854, by suppression under plenary powers (case ICZN 2115) (Diakonoff and Heppner, 1977), in Agonoxenidae.

Glyphipteryx Zeller, 1839:203

Glyphipterigidae

An unjustified emendation of *Glyphipterix* Hübner, [1825] [not *Glyphipteryx* Curtis, 1827 (Agonoxenidae)], now in Glyphipterigidae.

Glyphiptoryx [sic] Mann and Rogenhofer, 1878:500

Glyphipterigidae

A misspelling of *Glyphipterix* Hübner, [1825], now in Glyphipterigidae.

Glyphiteryx [sic] Fischer von Röslerstamm, 1841:233

Glyphipterigidae

A misspelling of *Glyphipterix* Hübner, [1825], now in Glyphipterigidae.

Glyphopteryx Herrich-Schäffer, 1854:92

Glyphipterigidae

An unjustified emendation of *Glyphipterix* Hübner, [1825], [not *Glyphipteryx* Curtis, 1827 (Agonoxenidae)], now in Glyphipterigidae.

Glyphptieryx [sic] Turati, 1879:203

Glyphipterigidae

A misspelling of *Glyphipterix* Hübner, [1825], now in Glyphipterigidae.

Glyphteryx [sic] Watt, 1920:439

Glyphipterigidae

A misspelling of *Glyphipterix* Hübner, [1825], now in Glyphipterigidae.

Glyphyteryx [sic] Hampson, 1918:387

Glyphipterigidae

A misspelling of *Glyphipterix* Hübner, [1825], now in Glyphipterigidae.

Gora Walker, 1862:89 Brachodidae

Type-species: *Gora aequalis* Walker, 1862:90, by monotypy. Type locality: Brazil [holotype ♀, UMO].

Originally described in Heliothidae [=Noctuidae]; subsequently transferred to Glyphipterygidae [sic] as a junior synonym of *Sagalassa* Walker, 1856, by Meyrick (1913b:31); transferred to Brachodidae as a junior subjective synonym of *Sagalassa* Walker, 1856, by Heppner (1981a:14).

Guaris [sic] Fernald, 1900:236 Choreutidae

A misspelling of *Gauris* Hübner, 1821, now a junior objective synonym of *Hemerophila* Hübner, [1817], in Choreutidae.

Heliomanes Sodoffsky, 1837:89 Noctuidae

An unjustified replacement name for *Anthophila* Ochsenheimer, 1816 [not *Anthophila* Haworth, 1811], now a junior synonym of *Porphyria* Hübner, [1821], in Noctuidae.

Heliostibes Zeller, 1874:434 *Oecophoridae

Type-species: *Heliostibes mathewi* Zeller, 1874:435, by monotypy. Type locality: Chile: Valparaiso [holotype ♂, BMNH].

Originally described in Tineacea; subsequently transferred to Gelechiidae by Butler (1883:76); transferred to Glyphipterygidae [sic] by Meyrick (1913b:29); hereby transferred to Oecophoridae: Oecophorinae.

Hemerophila Hübner, [1806]:[2] Choreutidae

Type-species: [*Phalaena*] *pariana* Clerck, 1759:pl. 10, fig. 9, by monotypy. Type locality: Europe [type lost?].

Originally described in Tortrices; now an unavailable synonym of *Choreutis* Hübner, [1825], in Choreutidae.

Hemerophila Hübner, [1806], is an unavailable name due to publication in a work rejected for nomenclatural purposes by Opinion 97 (ICZN, 1926).

Hemerophila Hübner, [1817]:pl. 213, fig. 1 Choreutidae

Type-species: *Phalaena* (*Tortrix*) *albertiana* Cramer, 1781:163, by monotypy. Type locality: Surinam [type lost?].

Originally described in Tortrices; subsequently transferred to Hemerophilidae by Walsingham (1910:257); transferred to Glyphipterygidae [sic] (as *Hemerophila* sensu Fernald, 1900) as a junior synonym of *Simaethis* Leach, 1815, by Meyrick (1913b:34); transferred to Choreutidae by Heppner (1977b:634) as a distinct genus.

Hemerophila sensu Fernald, 1900:239 Choreutidae

A redescription of *Hemerophila* Hübner, [1806], including *Simaethis vicarialis* Zeller, 1875:322 [= *Tortrix diana* Hübner, 1819–22]; now a junior subjective synonym of *Choreutis* Hübner, [1825], in Choreutidae.

Hemerophila Stephens, 1829a:43

Geometridae

Type-species: *Phalaena abruptaria* Thunberg, 1792:59, by monotypy. Type locality: Sweden [type lost?]. Preoccupied by *Hemerophila* Hübner, [1817] (Choreutidae).

Originally described in Geometrae [=Geometridae]; now a junior objective synonym of *Menophra* Moore, 1887, in Geometridae.

Hemerophila Stephens was redescribed twice by Stephens (Stephens, 1829b:125; 1831:189).

Heribeia Stephens, 1829a:49

Glyphipterigidae

Type-species: *Tinea forsterella* Fabricius, 1787:252, by subsequent designation of Westwood (1840:112). Type locality: Germany: Hamburg [type lost?].

Originally listed in 1829 and described in Yponomeutidae by Stephens (1834:261); subsequently transferred to Glyphipterygidae [sic] by Stainton (1854:163) as a junior subjective synonym of *Glyphipterix* Hübner, [1825].

Heribeia Stephens, 1829b:207, a redescription, was published in July, 1829, while the 1829a date is June, 1829.

Hierodoris Meyrick, 1912a:41

*Oecophoridae

Type-species: *Hierodoris iophanes* Meyrick, 1912a:42, by monotypy. Type locality: New Zealand: Wellington, North Island [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic]; hereby transferred to Oecophoridae: Oecophorinae.

Hilarographa Zeller, 1877:187

Tortricidae

Type-species: *Phalaena (Tortrix) swederiana* Stoll, 1790:75, by subsequent designation of Walsingham (1897a:51). Type locality: Surinam [type lost?].

Originally described as a subgenus of *Setiostoma* Zeller, 1875, in Tortricinae [=Tortricidae]; subsequently transferred to Glyphipterygidae [sic] as a distinct genus by Meyrick (1886: 286); transferred to the tribe Hilarographini of Tortricidae: Chlidanotinae by Diakonoff (1977a:76).

Hilarographa sensu Meyrick (1886:286)

Tortricidae

A redescription of *Hilarographa* Zeller, 1877, based on *Hilarographa zapyra* Meyrick (1886:286); now an objective synonym of *Thaumtographa* Walsingham, 1897, in the tribe Hilarographini of Tortricidae: Chlidanotinae.

Homadaula Lower, 1899:115

Plutellidae

Type-species: *Homadaula lasiochroa* Lower, 1899:115, by monotypy. Type locality: Australia: Broken Hill, New South Wales [lectotype unselected, SAMA?].

Originally described in Plutellidae; subsequently transferred to Glyphipterygidae [sic] by Clarke (1943:206); transferred to Plutellidae by Friese (1962:302).

Homadaula Meyrick, 1907:73

Plutellidae

Type-species: *Homadaula myriospila* Meyrick, 1907:73, by original designation. Type locality: Australia: West Australia [lectotype unselected, BMNH?].

A redescription of *Homadaula* Lower, 1899, in Plutellidae.

Homoplastis Meyrick, 1926a:162

*Oecophoridae?

Type-species: *Homoplastis agathoclea* Meyrick, 1926a:162, by monotypy. Type locality: [Malaysia]: Sarawak: Mt. Murud [holotype ♀, SMS?].

Originally described in Glyphipterygidae [sic]; hereby tentatively transferred to Oecophoridae: Oecophorinae.

Hoplophractis Meyrick, 1920b:326

Brachodidae

Type-species: *Hoplophractis heptachalca* Meyrick, 1920b:326, by monotypy. Type locality: Brazil: Obidos, Para [lectotype ♂ (Clarke, 1969:99), BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Brachodidae by Heppner (1979a:127).

Hyperperissa Walsingham, 1900b:546

*Immidae

Type-species: *Sidyma aurantiaca* Semper, 1899:501, by original designation. Type locality: Philippines: Mindanao [lectotype undesignated, BMNH].

Originally described in Gelechiidae [sic]; subsequently transferred as a junior synonym of *Imma* Walker, [1859], to Plutellidae by Meyrick (1906c:170) and to Glyphipterygidae [sic] by Meyrick (1913b:25); hereby transferred to Immidae as a junior subjective synonym of *Birhana* Walker, [1865], **new synonymy**.

Hypertropha Meyrick, 1881:208

Oecophoridae

Type-species: *Hypertropha thesaurella* Meyrick, 1881:209, by monotypy. Type locality: Australia: Parramatta, New South Wales [lectotype ♀ (Diakonoff, 1954:474), BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Copromorphidae by Meyrick (1906a:51); transferred to Glyphipterygidae [sic]: Hypertrophinae by Diakonoff (1954:274); transferred to Oecophoridae: Hypertrophinae by Common (1970b:819).

Idiothauma Walsingham, 1897a:49

Tortricidae

Type-species: *Idiothauma africanum* Walsingham, 1897a:50, by original designation. Type locality: French Congo [=Republic of the Congo]: Kangwé, Ogowé River [lectotype ♂ (present designation), BMNH].

Originally described in Glyphipteryginae of Hyponomeutidae [sic]; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Hilarographa* Zeller, 1877, by Meyrick (1913b:24); transferred to the tribe Hilarographini of Tortricidae: Chlidanotinae as a distinct genus by Heppner (1978a:53).

Imma Walker, [1859]:159

Immidae

Type-species: *Imma rugosalis* Walker, [1859]:195, by monotypy. Type locality: Ceylon [=Sri Lanka] [holotype ♂, BMNH].

Originally described in Herminidae [=Noctuidae]; subsequently transferred to Plutellidae sensu Meyrick (1906c:169); transferred to Glyphipterygidae [sic] by Meyrick (1910:464); transferred to Immidae by Heppner (1977a:129).

Inapha Walker, 1864:999

Gelechiidae

Type-species: *Inapha lampronialis* Walker, 1864:1000 [= *Thubana bisignatella* Walker, 1864:814], by monotypy. Type locality (*lampronialis*): [Malaysia]: Sarawak [holotype ♂, BMNH].

Originally described in Choreutidae; subsequently transferred to Gelechiidae by Meyrick (1925:234), as a junior subjective synonym of *Thubana* Walker, 1864:814.

Irianassa Meyrick, 1905:609

*Tortricidae

Type-species: *Irianassa sapphiropa* Meyrick, 1905:609, by monotypy. Type locality: Ceylon [=Sri Lanka]: Kandy [holotype ♂, BMNH].

Originally described in Plutellidae sensu Meyrick; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:23); hereby transferred to the tribe Hilarographini of Tortricidae: Chlidanotinae.

Iridostoma Meyrick, 1909b:425

*Yponomeutidae

Type-species: *Iridostoma ichthyopa* Meyrick, 1909b:425, by monotypy. Type locality: Ceylon [=Sri Lanka]: Peradeniya [holotype ♀, BMNH].

Originally described in Plutellidae sensu Meyrick; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:23); transferred to Yponomeutidae by Heppner (1981a:57).

Irinympha Meyrick, 1932:274

Glyphipterigidae

Type-species: *Irinympha aglaograpt* Meyrick, 1932:275, by monotypy. Type locality: Uganda: Entebbe [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic].

Jobula Walker, 1866:1888

*Immidae

Type-species: *Jobula semilinea* Walker, 1866:1889, by monotypy. Type locality: [Indonesia]: Sula [holotype ♂, UMO].

Originally described in Lithosiidae [=Arctiidae]; subsequently transferred to Hyponomeutidae [sic] by Walsingham (1897a:46); transferred to Plutellidae sensu Meyrick as a synonym of *Imma* Walker, [1859], by Meyrick, (1906c:170); transferred to Glyphipterygidae [sic] as a synonym of *Imma* Walker, [1859], by Meyrick (1913b:25); hereby transferred to Immidae as a junior subjective synonym of *Moca* Walker, 1863, **new synonymy**.

Jonaca Walker, 1863:457

Brachodidae

Type-species: *Jonaca compulsana* Walker, 1863:457 [= *Sagalassa valida* Walker, 1856:6], by monotypy. Type locality (*compulsana*): Brazil: Ega [=Tefé] [holotype ♂, BMNH].

Originally described in Choreutidae; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:31), as a synonym of *Sagalassa* Walker, 1856; transferred to Brachodidae as a junior subjective synonym of *Sagalassa* Walker, 1856, by Heppner (1981a:14).

Klimeschia Amsel, 1938:89

Douglesiidae

Type-species: *Klimeschia lutumella* Amsel, 1938:89, by original designation. Type locality: [Israel]: Jerusalem [holotype ♂, UMB].

Originally described in Douglesiidae.

Lamprystica Meyrick, 1914a:58

*Oecophoridae

Type-species: *Lamprystica purpurata* Meyrick, 1914a:58, by monotypy. Type locality: Formosa [=Taiwan]: Kosempo [lectotype unselected, HZMB].

Originally described in Glyphipterygidae [sic]; hereby transferred to Stathmopodini of Oecophoridae: Oecophorinae.

Lasiodictis Meyrick, 1912a:41

Oecophoridae

Type-species: *Lasiodictis melistoma* Meyrick, 1912a:41, by monotypy. Type locality: [India]: Khasi Hills, Assam [lectotype ♂ (Clarke, 1955b:438), BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Xyloryctidae [sic] by Clarke (1955a:19); transferred by Hodges ([1979]:8), to Oecophoridae: Autostichinae.

Lepidotarphius Pryer, 1877:235

Glyphipterigidae

Type-species: *Lepidotarphius splendens* Pryer, 1877:235 [= *Argyresthia perornatella* Walker, 1864:1040], by monotypy. Type locality (*splendens*): China: Shanghai [lectotype unselected, BMNH].

Originally described without family reference but noted to be related to *Butalis* (Gelechiidae); subsequently transferred to Glyphipterygidae [sic] as a synonym of *Glyphipteryx* [sic] Hübner, [1825], by Meyrick (1913b:41); here considered a distinct genus in Glyphipterigidae.

Lithariapteryx Chambers, 1876:217

Heliodinidae

Type-species: *Lithariapteryx abroniaeella* Chambers, 1876:217, by monotypy. Type locality: USA: Edgerton, Colorado [holotype, MCZ?].

Originally described in Tineina; subsequently transferred to Glyphipterygidae [sic] by Riley (1891:104); transferred to Heliodinidae as a synonym of *Heliodines* Stainton, 1854, by Meyrick (1913b:17); now considered a distinct genus in Heliodinidae.

Litobrenthia Diakonoff, 1978:28

Choreutidae

Type-species: *Brenthia japonica* Issiki, 1930:424, by original designation.

Type locality: Japan: Hasimoto [lectotype (Diakonoff, in press), USNM].

Originally described in Choreutidae.

Lotisma Busck, 1909:98

Copromorphidae

Type-species: *Sciaphila trigonana* Walsingham, 1879:22, by original designation. Type locality: USA: Mendocino, California [lectotype ♀ (present designation), BMNH].Originally described as being related to *Hemerophila* Hübner; subsequently transferred to Glyphipterygidae [sic] by Busck (1925:46); transferred to Copromorphidae by Heppner (1978a:49).**Loxotrochis** Meyrick, 1906c:205

*Immidae

Type-species: *Loxotrochis sepias* Meyrick, 1906c:205, by monotypy. Type locality: Brazil: Espirito Santo [holotype ♂, BMNH].

Originally described in Plutellidae sensu Meyrick; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:25); hereby transferred to Immidae.

Meyrick (1906c) originally indicated the type locality to be "Espirito Santo, New Hebrides" but he later corrected this (Meyrick, 1907:108) to read Espirito Santo, Brazil.

Lygronoma Meyrick, 1913a:100

Oecophoridae

Type-species: *Lygronoma sporimaea* Meyrick, 1913a:100, by monotypy. Type locality: British Guiana [=Guyana]: Bartica [lectotype ♂ (Clarke, 1969:175), BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred by Heppner (1981a:57), to Oecophoridae: Stenomatinae; hereby transferred to Oecophoridae: Oecophorinae (Becker, pers. comm.).

Machlotica Meyrick, 1909a:36

Glyphipterigidae

Type-species: *Machlotica chrysodeta* Meyrick, 1909a:37, by original designation. Type locality: Bolivia: Songo [=Zongo] [holotype ♀, BMNH].

Originally described in Plutellidae; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:23).

Maclotica [sic] Busck, 1915:87

Glyphipterigidae

A misspelling of *Machlotica* Meyrick, 1909.**Macropia** Costa, [1836]:[196]

Choreutidae

Type-species: *Asopia incisalis* Treitschke, 1829:157 [= *Tortrix nemorana* Hübner, [1796–99]:pl. 1, fig. 3], by subsequent designation of Heppner (1978b:159). Type locality (*incisalis*): [Europe] [type lost?].

Originally described in Pyralidae; subsequently transferred to Choreuti-

dae as a junior subjective synonym of *Eutromula* Frölich, 1828, by Heppner (1978b:159); now a junior subjective synonym of *Choreutis* Hübner, [1825] (Heppner, 1981a:53).

Macropia Costa, [1836], is a senior homonym of *Macropia* Malloch, 1930 (Diptera) (Heppner, 1978b).

Mattea Duckworth, 1966:2

Oecophoridae

Type-species: *Cryptolechia phoenissa* Butler, 1883:81, by original designation. Type locality: Chile: Corral [holotype ♂, BMNH].

Originally described in Oecophoridae. *Mattea* Duckworth, 1966, is a junior objective synonym of *Tyriomorpha* Meyrick, 1918, as indicated by Clarke (1979:142), in Oecophoridae: Oecophorinae; now also a junior subjective synonym of *Pachyphoenix* Butler, 1883, **new synonymy** (Becker, pers. comm).

Melanoxena Dognin, 1910:121

Choreutidae

Type-species: *Melanoxena falsissima* Dognin, 1910:122, by original designation. Type locality: Colombia: San Antonio, near Cali [lectotype ♂ (present designation), USNM].

Originally described in Tineidae; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Rhobonda* Walker, 1863, by Meyrick (1913b:31); transferred to Choreutidae by Heppner (1981a:56), as a distinct genus in Choreutidae.

Metapodistis Meyrick, 1933:372

Glyphipterygidae

Type-species: *Metapodistis chrysosema* Meyrick, 1933:372, by monotypy. Type locality: Solomon Is.: Tulagi [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic]; now a junior subjective synonym of *Carmentina* Meyrick, 1930 (Heppner, 1982c).

Methypsa Butler, 1875:324

*Immidae

Type-species: *Hypsa saturata* Walker, [1865]:217, by original designation. Type locality: [Malaysia?] [holotype ♂, BMNH].

Originally described in Lithosiidae [=Arctiidae]; subsequently transferred to Plutellidae sensu Meyrick as a synonym of *Imma* Walker, [1859], by Meyrick (1906c:170); transferred to Glyphipterygidae [sic] as a synonym of *Imma* Walker, [1859], by Meyrick (1913b:25); hereby transferred to Immidae as junior subjective synonym of *Birrhana* Walker, [1865], **new synonymy**.

Microaethia Chambers, 1878:76

Choreutidae

Type-species: *Microaethia amphicarpeoeana* Chambers, 1878:76, by monotypy [nomen nudum, published in synonymy].

Microaethia Chambers, 1878, is not an available name as it was published in synonymy under *Brenthia* Clemens, 1860, now in Choreutidae.

Mictocommosis Diakonoff, 1977b:8 Tortricidae

Type-species: *Simaethis nigromaculata* Issiki, 1930:423, by original designation. Type locality: Japan: Mt. Iwawakisan, Honshu [holotype ♀, USNM].

Originally described in the tribe Hilarographini of Tortricidae: Chlidanotinae.

Mictopsichia Hübner, [1825]:374 Tortricidae

Type-species: *Phalaena (Tortrix) hubneriana* Stoll, 1787:41, by subsequent designation of Walsingham (1914:303). Type locality: [Surinam] [type lost?].

Originally described in Tortrices Lascivae; subsequently transferred to Glyphipteryginae [sic] of Hyponomeutidae [sic] by Walsingham (1897a:54); transferred to Glyphipterygidae [sic] by Meyrick (1913b:24); transferred to the tribe Hilarographini of Tortricidae: Chlidanotinae by Diakonoff (1977a:76).

Mictopsychia [sic] Riley, 1889:158 Tortricidae

A misspelling of *Mictopsichia* Hübner, [1825].

Mictropsichia [sic] Heppner, 1978a:53 Tortricidae

A misspelling of *Mictopsichia* Hübner, [1825].

Milliera [sic] Le Marchand, 1937:192 Choreutidae

A misspelling of *Millieria* Ragonot, 1874.

Milliereia Spuler, 1910:298 Choreutidae

An unjustified emendation of *Millieria* Ragonot, 1874.

Millieria Ragonot, 1874:173 Choreutidae

Type-species: *Choreutis dolosana* Herrich-Schäffer, 1854:95, by original designation. Type locality: Hungary [type lost?].

Originally described in Choreutidae.

Millieroa [sic] Le Marchand, 1937:192 Choreutidae

A misspelling of *Millieria* Ragonot, 1874.

Miscera Walker, 1863:457 Brachodidae

Type-species: *Miscera resumptana* Walker, 1863:458, by monotypy. Type locality: Australia: Moreton Bay, Queensland [holotype ♂, BMNH].

Originally described in Choreutidae; subsequently transferred to Hyponomeutinae [sic] of Plutellidae by Meyrick (1907:100); transferred to Glyphipterygidae [sic] as a synonym of *Sagalassa* Walker, 1856, by Meyrick (1913b:31); transferred to Brachodidae as a distinct genus by Heppner (1979a:127).

Moca Walker, 1863:102

*Immidae

Type-species: *Moca velutina* Walker, 1863:102, by subsequent designation of Meyrick (1906c:170). Type locality: Ceylon [=Sri Lanka] [holotype ♂, BMNH].

Originally described in Galleridae [=Pyrilidae]; subsequently transferred to Plutellidae sensu Meyrick by Meyrick (1906c:170), as a synonym of *Imma* Walker, [1859]; transferred to Glyphipterygidae [sic] as a synonym of *Imma* Walker, [1859], by Meyrick (1913b:25); hereby transferred to Immidae as a distinct genus.

Mylocera Turner, 1897:27

Oecophoridae

Type-species: *Mylocera tenebrifera* Turner, 1897:27, by monotypy. Type locality: Australia: Brisbane, Queensland [holotype ♂, SAMA].

Originally described in Xyloryctidae; later associated with Glyphipterigidae; now in Oecophoridae: Xyloryctinae.

Myrsila Boisduval, [1875]:433

Glyphipterigidae

Type-species: *Myrsila auripennis* Boisduval, [1875]:433, by monotypy. Type locality: Brazil: Para [holotype, UMO].

Originally described in Sesiidae; transferred to Glyphipterigidae by Heppner (1981a:44).

Napecoetes Turner, 1913:218

*Plutellidae

Type-species: *Napecoetes crossospila* Turner, 1913:218, by monotypy. Type locality: Australia: Montville, Queensland [holotype ♂, ANIC].

Originally described in Glyphipteryginae [sic] of Plutellidae; hereby transferred to Plutellidae.

Neomachlotica Heppner, 1981c:479

Glyphipterigidae

Type-species: *Neomachlotica spiraea* Heppner, 1981c:481, by original designation. Type locality: Florida: Fisheating Creek, Glades Co. [holotype ♂, USNM].

Originally described in Glyphipterigidae.

Nesotropha Turner, 1926b:110

*Yponomeutidae

Type-species: *Nesotropha pygmaeodes* Turner, 1926b:110, by monotypy. Type locality: Australia: Cradle Mtn., Tasmania [lectotype unselected, ANIC].

Originally described in Arctiidae [sic]; later associated with a Glyphipterigidae genus; hereby transferred to Yponomeutidae as a junior subjective synonym of *Tanaoctena* Turner, 1913, new synonymy (Common, pers. comm.).

Nexosa Diakonoff, 1977b:12

Tortricidae

Type-species: *Mictopsichia marmarastra* Meyrick, 1932:273, by original designation. Type locality: [Indonesia]: Java [holotype ♂, BMNH].

Originally described in the tribe Hilarographini of Tortricidae: Chlidanotinae.

Nigilgia Walker, 1863:511

Brachodidae

Type-species: *Nigilgia adjectella* Walker, 1863:512, by monotypy. Type locality: Sierra Leone [holotype ♀, BMNH].

Originally described in Tineidae; subsequently transferred to Atychiadae [=Brachodidae] by Walsingham (1891:80), as a synonym of *Phycodes* Guenée, 1852; transferred to Glyphipterygidae [sic] as a synonym of *Phycodes* Guenée, 1852, by Meyrick (1913b:32); transferred to Brachodidae as a distinct genus by Heppner (1979a:127).

Nigilica [sic] Turner, 1929:306

Brachodidae

A misspelling of *Nigilgia* Walker, 1863.

Orchemia Guenée, 1845:192

Tortricidae

Type-species: *Orchemia gallicana* Guenée, 1845:192, by subsequent designation of Bruand (1850a:96). Type locality: France [type, MNHP?].

Originally described in Tortrices; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Simaethis* Leach, 1815, by Meyrick (1913b:34); currently considered to be a junior subjective synonym of *Cydia* Hübner, [1825], in Tortricidae.

Orchemia sensu Fernald, 1900:238

Choreutidae

Originally described in Choreutidae as *Orchemia* Guenée but with only one included species (*Tortrix diana* Hübner, [1819–22]); now a junior subjective synonym of *Choreutis* Hübner, [1825], in Choreutidae.

Ordrupia Busck, 1911:228

Copromorphidae

Type-species: *Ordrupia friserella* Busck, 1911:228, by original designation. Type locality: French Guiana: St. Jean, Maroni River [holotype ♀, USNM].

Originally described in Hemerophilidae [=Choreutidae]; subsequently transferred to Copromorphidae by Meyrick (1926:242).

Ordupia [sic] Busck, 1911:228

Copromorphidae

An original multiple spelling of *Ordrupia* Busck, 1911, corrected by Busck (1912:8) and now in Copromorphidae.

Orosana Walker, 1863:458

Pyrallidae

Type-species: *Orosana ophideresana* Walker, 1863:459, by subsequent designation of Diakonoff (1954:285). Type locality: Australia, Hindustan, and Ceylon [lectotype unselected, BMNH].

Originally described in Choreutidae; subsequently transferred to Pyralidae by Moore (1885:268) as a junior subjective synonym of *Heliothela* Guenée, 1854, now in Pyralidae: Scopariinae.

Orosoma [sic] Cotes, 1889:666 Pyralidae

A misspelling of *Orosana* Walker, 1863 [= *Heliothela* Guenée, 1854], now in Pyralidae.

Oxytrophia Diakonoff, 1954:488 Oecophoridae

Type-species: *Hypertrophia ametalla* Turner, 1898:202, by original designation. Type locality: Australia: Armidale, New South Wales [holotype ♂, ANIC].

Originally described in Hypertrophinae of Glyphipterygidae [sic]; now in Oecophoridae: Hypertrophinae.

Pachyphoenix Butler, 1883:81 *Oecophoridae

Type-species: *Pachyphoenix sanguinea* Butler, 1883:81, by monotypy. Type locality: Chile: Corral [holotype ♂, BMNH].

Originally described in Gelechiidae; subsequently associated with Glyphipterigidae; hereby transferred to Oecophoridae: Oecophorinae (Becker, pers. comm.).

Palamernis Meyrick, 1906c:205 Brachodidae

Type-species: *Palamernis canonitis* Meyrick, 1906c:206, by monotypy. Type locality: India: Simla [lectotype ♂ (Clarke, 1969:187), BMNH].

Originally described in Plutellidae sensu Meyrick subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:29); transferred to Brachodidae by Heppner (1979a:128), as a junior subjective synonym of *Brachodes* Guenée, 1845.

Pantosperma Meyrick, 1888:89 Glyphipterigidae

Type-species: *Pantosperma holochalca* Meyrick, 1888:89, by monotypy. Type locality: New Zealand: Makatoku [lectotype ♂ (present designation), BMNH].

Originally described in Glyphipterygidae [sic]; subsequently considered a synonym of *Glyphipterix* Hübner, [1825]; here considered as a distinct genus.

Paraprays Rebel, 1910:13 Plutellidae

Type-species: *Paraprays punctigera* Rebel, 1910:13, by monotypy. Type locality: [USSR]: Altai Mts. [Kirghiz SSR] [lectotype, NHMV?].

Originally described in Hyponomeutidae [sic]; subsequently transferred to Plutellidae by Friese (1960:23); transferred to Glyphipterygidae [sic] as a synonym of *Homadaula* Lower, 1899, by Clarke (1968:228); transferred to Plutellidae as a junior subjective synonym of *Homadaula* Lower, 1899, by Heppner and Dekle (1975:1).

Penthocrates Meyrick, 1934:523

*Limacodidae

Type-species: *Penthocrates bigenita* Meyrick, 1934:523, by monotypy.
 Type locality: [Indonesia]: Koetoardjo, Rio Awibowo, Java [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic]; transferred to Heterogeneidae [sic] by Meyrick (1934:523) following the original description; hereby transferred to Limacodidae.

Peotyle Diakonoff, 1978:23

Choreutidae

Type-species: *Choreutis atmodesma* Meyrick, 1933:371, by original designation. Type locality: [India]: Killanmarg, Kashmir [lectotype ♂ (Clarke, 1969:43), BMNH].

Originally described in Choreutidae.

Peritropha Diakonoff, 1954:278

Oecophoridae

Type-species: *Peritropha oligodrachma* Diakonoff, 1954:280, by original designation. Type locality: Australia: Billopp [holotype ♂, BMNH].

Originally described in Hypertrophinae of Glyphipterygidae [sic]; now in Oecophoridae: Hypertrophinae.

Perittia Stainton, 1854:177

Elachistidae

Type-species: *Aphelosetia obscurepunctella* Stainton, 1848:2164, by monotypy. Type locality: England [type, BMNH?].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Elachistidae by Meyrick (1895:685).

Phalerarcha Meyrick, 1913a:100

Glyphipterigidae

Type-species: *Phalerarcha chrysorma* Meyrick, 1913a:101, by monotypy. Type locality: British Guiana [=Guyana]: Bartica [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic].

Philocoristis Meyrick, 1927c:102

*Heliodinidae

Type-species: *Philocoristis catachalca* Meyrick, 1927c:102, by monotypy. Type locality: Samoa: Upolu, Malololelei [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic], hereby transferred to Heliodinidae.

Philodoria Walsingham, 1907:717

Gracillariidae

Type-species: *Philodoria succedanea* Walsingham, 1907:717, by original designation. Type locality: Hawaii: Heleakala, Maui [lectotype unselected, BMNH].

Originally described in Tineidae; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:40); transferred to Gracilariadae [sic] by Swezey (1934:524).

Philpottia Meyrick, 1916:416

*Plutellidae

Type-species: *Philpottia iridoxa* Meyrick, 1916:417, by monotypy. Type locality: New Zealand: Mt. Burns, Hunter Mts. [lectotype ♀, BMNH].

Originally described in Glyphipterygidae [sic]; hereby transferred to Plutellidae.

Philpottia Meyrick, 1916, is a junior homonym of *Philpottia* Brown, 1915, (Coleoptera) and is now replaced by *Charixena* Meyrick, 1920.

Phryganostola Meyrick, 1881:248

Glyphipterigidae

Type-species: *Phryganostola drosophaes* Meyrick, 1881:249, by subsequent designation of Meyrick (1914d:28). Type locality: Australia: Parramatta, [New South Wales] [lectotype unselected, BMNH].

Originally described in Glyphipterygidae [sic].

Phycodes Guenée, 1852:389

Brachodidae

Type-species: *Phycodes hirudinicornis* Guenée, 1852:389 [= *Chimaera radiata* Ochsenheimer, 1808:5], by monotypy. Type locality (*hirudinicornis*): “Indies Orientales” [holotype ♂, MNHP?].

Originally described in Hyblaeidae; subsequently transferred to Atychiidae [sic] [=Brachodidae] by Walsingham (1891:78); transferred to Glyphipterygidae [sic] by Meyrick (1913b:32); transferred to Brachodidae by Heppner (1979a:127).

Picrodoxa Meyrick, 1923:617

*Epermeniidae

Type-species: *Picrodoxa harpodes* Meyrick, 1923:617, by monotypy. Type locality: India: Palnis [lectotype ♀ (Clarke, 1969:192), BMNH].

Originally described in Glyphipterygidae [sic]; hereby transferred to Epermeniidae.

Piestoceros Meyrick, 1907:94

*Yponomeutidae

Type-species: *Incurvaria conjunctella* Walker, 1863:491, by monotypy. Type locality: Australia [holotype ♂, BMNH].

Originally described in Plutellidae; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:32); hereby transferred to Yponomeutidae.

Pingrassa Walker, [1859]:266

*Immidae

Type-species: *Pingrassa accuralis* Walker, [1859]:227, by monotypy. Type locality: Ceylon [=Sri Lanka] [holotype ♀, BMNH].

Originally described in Herminidae [=Noctuidae]; subsequently transferred to Plutellidae as a synonym of *Imma* Walker, [1859], by Meyrick (1906c:170); hereby transferred to Immidae as a junior subjective synonym of *Imma* Walker, [1859].

***Plotheia* Walker, 1863:460**

Noctuidae

Type-species: *Plotheia innotabilis* Walker, 1863:461, by monotypy. Type locality: Sarawak [holotype ♀, BMNH].

Originally described in Choreutidae; now in Noctuidae as a junior objective synonym of *Thopelia* Nye, 1975:480, a replacement name.

Plotheia Walker, 1863, is a junior homonym of *Plotheia* Walker, [1858] (Noctuidae).

***Polygiton* Diakonoff, 1955:26**

Oecophoridae

Type-species: *Polygiton pachypus* Diakonoff, 1955:28, by original designation. Type locality: New Guinea: Araucaria Camp [holotype ♂, RMNL].

Originally described in Glyphipterygidae [sic], subfamily Hypertrophinae; now a subfamily of Oecophoridae.

***Polyphlebia* Felder, 1874:8 (pl. 102, f. 38)**

Brachodidae

Type-species: *Polyphlebia atychioides* Felder, 1874:8 (plate 102, figure 38) [= *Aclytia buprestoides* Walker, [1865]:101], by monotypy. Type locality (*atychioides*): South America [type, NHMV?].

Originally described in Tineidae; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Sagalassa* Walker, 1856, by Meyrick (1913b:31); transferred to Brachodidae as a distinct genus by Heppner (1979a:127).

***Porpe* Hübner, [1825]:373**

Choreutidae

Type-species: *Porpe fibrana* Hübner, [1825]:373 [= *Tinea vibrana* Hübner, [1811–13]: plate 32, figure 202; = *Tinea bjerkandrella* Thunberg, 1784:24], by monotypy. Type locality (*fibrana*): [Europe] [type lost?].

Originally described in Tortrices Lascivae; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Choreutis* Hübner, [1825], by Meyrick (1913b:38); transferred to Hemerophilidae [=Choreutidae] by Walsingham (1914:309), as a distinct genus; transferred to Glyphipterigidae by Bradley (1972:12) as a synonym of *Tebenna* Billberg, 1820; transferred to Choreutidae as a junior subjective synonym of *Tebenna* Billberg, 1820, by Heppner (1977b:635).

***Probolacma* Meyrick, 1927a:362**

Plutellidae

Type-species: *Probolacma melanoclista* Meyrick, 1927a:362, by monotypy. Type locality: USA: Alpine, [Brewster Co.], Texas [holotype ♀, BMNH].

Originally described in Hyponomeutidae [sic]; subsequently transferred to Glyphipterygidae [sic] by McDunnough (1939:84); transferred to Plutellidae as a junior subjective synonym of *Ellabella* Busck, 1925, by Heppner (1978a:50).

Procerata Berthold, 1827:484

Brachodidae

Type-species: *Pyrallis saldonana* Fabricius, 1787:232 [as “*soldana*” [sic] Berthold] [= *Sphinx appendiculata* Esper, 1783:227], by monotypy. Type locality (*saldonana*): Europe [type lost?].

Originally described in Pyrales; subsequently a nomen oblitum; treated as a nomen oblitum in synonymy of *Brachodes* Guenée, 1845, in Brachodidae by Heppner (1981a:13) [unused since Wocke (1871:266)].

Prochoreutis Diakonoff and Heppner, 1980:196

Choreutidae

Type-species: *Pyrallis myllerana* Fabricius, 1794:277, by original designation. Type locality: Sweden [type lost?].

Originally described in Choreutidae as a new name for *Choreutis* of authors [not *Choreutis* Hübner, 1825].

Prochoreutis Heppner, 1981a:58

Choreutidae

Type-species: *Pyrallis myllerana* Fabricius, 1794:277, by original designation. Type locality: Sweden [type lost?].

Redescription of *Prochoreutis* Diakonoff and Heppner, 1980, as a new name for *Choreutis* of authors [not *Choreutis* Hübner 1825].

Protosynaema Meyrick, 1886:173

Plutellidae

Type-species: *Protosynaema eratopis* Meyrick, 1886:174, by subsequent designation of Fletcher (1929:187). Type locality: New Zealand: Otira Gorge [lectotype unselected, BMNH].

Originally described in Plutellidae and noted to be related to *Glyphipteryx* [sic] Hübner (Glyphipterigidae); now returned to Plutellidae.

Pseudotortrix Turner, 1900:15

*Immidae

Type-species: *Pseudotortrix acosma* Turner, 1900:16, by monotypy. Type locality: Australia: Brisbane, Queensland [lectotype unselected, ANIC].

Originally described in Plutellidae; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Imma* Walker, [1859], by Meyrick (1913b:25); hereby transferred to Immidae as a junior subjective synonym of *Imma* Walker, [1859].

Ptochaula Meyrick, 1920b:325

*Immidae

Type-species: *Ptochaula niphadopa* Meyrick, 1920b:325, by monotypy. Type locality: [India]: Khasis, Assam [lectotype ♂ (Clarke, 1969:195), BMNH].

Originally described in Glyphipterygidae [sic]; hereby transferred to Immidae.

Rhabdocrates Meyrick, 1931:183

Glyphipterigidae

Type-species: *Rhabdocrates sporomantis* Meyrick, 1931:184, by monotypy. Type locality: Peru: Jurimaguas [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic].

Rhipismia Reutii, 1898:180 Choreutidae
 An emendation of *Ripismia* Wocke, [1876] [= *Millieria* Ragonot, 1874].

Rhobonda Walker, 1863:424 Choreutidae

Type-species: *Rhobonda gaurisana* Walker, 1863:425, by monotypy.
 Type locality: Brazil: Rio de Janeiro [holotype ♀, BMNH].

Originally described in Tortricidae; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:34); transferred to Hemerophilidae [= Choreutidae] by Walsingham (1914:314); now in Choreutidae.

Rhobonda Walker, 1864:802 Gelechiidae

Type-species: *Rhobonda punctatella* Walker, 1864:802, by monotypy.
 Type locality: Brazil: Ega [=Tefê], [Amazonas] [holotype ♀, BMNH?].

Originally described in Gelechidae [sic].

Rhobonda Walker, 1864, is a junior homonym of *Rhobonda* Walker, 1863 (Choreutidae), and is now considered a junior subjective synonym of *Dichomeris* Hübner, [1825], in Gelechiidae. The name *Carna* Walker, 1864:1038, proposed as a replacement name for *Rhobonda* Walker, 1864, is a junior homonym of *Carna* Gistel, 1848 (Echinodermata).

Ripismia Wocke, [1876]:399 *Choreutidae

Type-species: *Choreutis dolosana* Herrich-Schäffer, 1854:95, by monotypy. Type locality: Hungary [type lost?].

Originally described in Glyphipterygidae [sic]; subsequently considered in Glyphipterygidae [sic] as a junior synonym of *Millieria* Ragonot, 1874, by Meyrick (1913b:38); hereby transferred to Choreutidae as a junior subjective synonym of *Millieria* Ragonot, 1874.

Roeslerstammia Zeller, 1839:202 Yponomeutidae

Type-species: *Alucita erxlebella* Fabricius, 1787:256, by monotypy. Type locality: Germany: Göttingen [type?].

Originally described in Glossata (*Alucita*); subsequently transferred to Glyphipterygidae [sic] by Stainton (1854:172); transferred to Tineidae by Meyrick (1895:770); transferred to Acrolepiidae by Spuler (1910:454); transferred to Hyponomeutidae [sic] by Meyrick (1928:743).

Sagalassa Walker, 1856:5 Brachodidae

Type-species: *Sagalassa robusta* Walker, 1856:6, by subsequent designation of Meyrick (1914d:15). Type locality: Brazil: Para [lectotype unselected, BMNH].

Originally described in Stygiidae [=Cossidae]; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:31); transferred to Brachodidae by Heppner (1979a:127).

Saphtha [sic] Walsingham, 1900b:567 Choreutidae

A misspelling of *Saptha* Walker, 1864.

Saptha Walker, 1864:1015

Choreutidae

Type-species: *Saptha divitiosa* Walker, 1864:1015, by monotypy. Type locality: [Indonesia]: Ceram [holotype ♀, BMNH].

Originally described in Tineidae; subsequently transferred to Plutellidae by Meyrick (1905:610); transferred to Glyphipterygidae [sic] as a synonym of *Tortyra* Walker, 1863, by Meyrick (1913b:33); transferred to Hemerophilidae [=Choreutidae] as a synonym of *Tortyra* Walker, 1863, by Walingham (1914:312); now a distinct genus in Choreutidae (Heppner, 1981a:55).

Scaptesylix Hampson, 1895:283

*Immidae

Type-species: *Scaptesylix hemichryseis* Hampson, 1895:283, by original designation. Type locality: Burma: Donaut Range [holotype ♀, BMNH].

Originally described in Zygaenidae; subsequently transferred as a synonym of *Imma* Walker, [1859], to Plutellidae by Meyrick (1906c:170) and to Glyphipterygidae [sic] by Meyrick (1913b:25); hereby transferred to Immidae as a junior subjective synonym of *Bursadella* Snellen, 1880, **new synonymy**.

Sesiomorpha Snellen, 1885:111

Zygaenidae

Type-species: *Sesiomorpha abnormis* Snellen, 1885:112 [= *Syntomis vacua* Walker, [1865]:75], by monotypy. Type locality (*abnormis*): [Indonesia]: Bantimoreng, Celebes [lectotype unselected, RMNL?].

Originally described in Tineidae; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Burlacena* Walker, [1865], by Meyrick (1913b:25); transferred to Zygaenidae as a junior subjective synonym of *Burlacena* Walker, [1865], by Heppner (1981a:15).

Setiostoma Felder and Rogenhofer, 1875:18

*Glyphipterigidae

Type-species: *Setiostoma flaviceps* Felder and Rogenhofer, 1875:18 (pl. 138, fig. 1), by monotypy. Type locality: Amazonas [Brazil] [lectotype unselected, BMNH].

Originally described in Tineae; subsequently transferred to Glyphipterygidae [sic] (as *Setiostoma* Zeller, 1875) by Meyrick (1913b:13); thereafter forgotten in lieu of *Setiostoma* Zeller, 1875 (subsequently placed in Oecophoridae: Stenomatinae); hereby placed in Glyphipterigidae as a junior subjective synonym of *Ussara* Walker, 1864 (Becker, pers. comm.).

Setiostoma Zeller, 1875:324

Oecophoridae

Type-species: *Setiostoma xanthobasis* Zeller, 1875:325, by subsequent designation of Meyrick (1914d:4). Type locality: USA: [Dallas], Texas [holotype ♂, MCZ].

Originally described in Choreutina [=Choreutidae]; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:13); transferred to Stenomidae by Busck (1922:279); now in the subfamily Stenomatinae of Oeco-

phoridae as a junior objective synonym of *Rectiostoma* Becker, (Type-species: *Setiostoma xanthobasis* Zeller, 1875 [by present designation]).

Setiostoma Zeller, 1875 (September 1875) is a junior homonym of *Setiostoma* Felder and Rogenhofer, 1875 (June 1875) [= *Ussara* Walker, 1864 (Glyphipterigidae)].

Sezeris Walker, 1863:509

Psychidae

Type-species: *Sezeris conflictella* Walker, 1863:509 [= *Cebysa leucotelus* Walker, 1854:486], by monotypy. Type locality (*conflictella*): Australia: Tasmania [holotype ♂, BMNH].

Originally described in Tineidae; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Cebysa* Walker, 1854, by Meyrick (1913b:32); now considered to be a junior subjective synonym of *Cebysa* Walker, 1854, in Psychidae.

Siamethis [sic] Klimesch, 1968:150

Choreutidae

A misspelling of *Simaethis* Leach, 1815 [= *Anthophila* Haworth, 1811].

Simaethis Leach, 1815:135

Choreutidae

Type-species: *Tortrix dentana* Hübner, [1796–99]: plate 1, figure 4 [= *Phalaena* (*Tortrix*) *fabriciana* Linnaeus, 1767:880], by monotypy. Type locality (*dentana*): [Europe] [type lost?].

Originally described in Tortricina [sic]; subsequently transferred to Pyralidae by Stephens (1829b:161); transferred to Choreutidae by Walker (1863:450); transferred to Glyphipterygidae [sic] by Meyrick (1913b:34); transferred to Choreutidae as a junior subjective synonym of *Anthophila* Haworth, [1811], by Heppner (1977b:633).

Simaetis [sic] Kautz, 1930:28

Choreutidae

A misspelling of *Simaethis* Leach, 1815 [= *Anthophila* Haworth, 1811].

Simethis [sic] Bleszynski, Razowski,
and Zukowski, 1965:413

Choreutidae

A misspelling of *Simaethis* Leach, 1815 [= *Anthophila* Haworth, 1811].

Simoethis [sic] Desmarest, 1848:617

Choreutidae

A misspelling of *Simaethis* Leach, 1815 [= *Anthophila* Haworth, 1811].

Sisyroctenis Meyrick, 1936b:106

Brachodidae

Type-species: *Sisyroctenis hemicamina* Meyrick, 1936b:106, by monotypy. Type locality: Peru: Marcapata [holotype ♀, DEI].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Brachodidae as a junior subjective synonym of *Callatolmis* Butler, 1877, by Heppner (1981a:14).

Sobareutis Meyrick, 1910:469

Heliodinidae

Type-species: *Sobareutis conchophanes* Meyrick, 1910:470, by monotypy. Type locality: [Malaysia] Kuching, [Sarawak] [holotype ♂, lost?].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Heliodinidae by Meyrick (1913b:18).

(The unique holotype has not been located for study to determine if the genus correctly belongs in Heliodinidae [it may belong to Oecophoridae: Stathmopodini]).

Spilogenes Meyrick, 1938:19

Plutellidae

Type-species: *Spilogenes chalazombra* Meyrick, 1938:19, by monotypy. Type locality: China: Likiang [lectotype ♂ (Clarke, [1965]:384), BMNH].

Originally described in Hyponomeutidae [sic]; subsequently transferred to Xyloryctidae by Clarke (1955:24); transferred to Plutellidae as a junior subjective synonym of *Ellabella* Busck, 1925, by Heppner (1978a:50).

Staintonia Staudinger, 1859:250

Oecophoridae

Type-species: *Staintonia medinella* Staudinger, 1859:250, by monotypy. Type locality: Spain: Chiclana [lectotype unselected, ZMHB].

Originally described without family reference except as being related to *Butalis* (Gelechiidae); subsequently associated with *Glyphipteryx* [sic] Hübner, [1825], by Erschoff (1877:347); transferred to Heliodinidae by Meyrick (1913b:15) as a junior subjective synonym of *Eretmocera* Zeller, 1852, now a genus in Stathmopodini of Oecophoridae: Oecophorinae.

Sthenistis Hampson, 1896:541

*Immidae

Type-species: *Sthenistis gyrtiformis* Hampson, 1896:541, by original designation. Type locality: Ceylon [=Sri Lanka] [lectotype unselected, BMNH].

Originally described in Noctuidae; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Imma* Walker, [1859], by Meyrick (1913b:25); hereby transferred to Immidae as a distinct genus.

Stichotactis Meyrick, 1930b:562

Plutellidae

Type-species: *Stichotactis calamitosa* Meyrick, 1930b:563, by monotypy. Type locality: Sudan: Gendettu [lectotype ♀ (Clarke, 1969:200), BMNH].

Originally described in Hyponomeutidae [sic]; subsequently transferred to Glyphipterygidae [sic] by Clarke (1955:24); transferred to Plutellidae by Heppner and Dekle (1975:1) as a junior subjective synonym of *Homadaula* Lower, 1899.

Symaethis [sic] Bruand, 1850a:101

Choreutidae

A misspelling of *Simaethis* Leach, 1815, now a synonym of *Anthophila* Haworth, [1811], in Choreutidae.

Symphorostola Meyrick, 1927c:376

Oecophoridae

Type-species: *Symphorostola encomias* Meyrick, 1927c:376, by monotypy. Type locality: [Indonesia]: Soekaranda Urwald, Sumatra [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic]; transferred to Oecophoridae: Xyloryctinae by Heppner (1981a:57).

Synechodes Turner, 1913:200

Brachodidae

Type-species: *Synechodes coniophora* Turner, 1913:200, by monotypy. Type locality: Australia: Kuranda, Queensland [holotype ♂, ANIC].

Originally described in Hyponomeutinae [sic] of Plutellidae as being related to *Miscera* and *Tortyra*; transferred to Brachodidae by Heppner (1979a:127).

Taeniostola Meyrick, 1920b:326

Glyphipterigidae

Type-species: *Taeniostola celophora* Meyrick, 1920b:327, by monotypy. Type locality: Brazil: Rio Trombetas [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic].

Taeniostola Meyrick, 1920, is a junior homonym of *Taeniostola* Bezzi, 1913 (Diptera), and is now a synonym of *Taeniostolella* Fletcher, 1940, in Glyphipterigidae.

Taeniostolella Fletcher, 1940:109

Glyphipterigidae

Type-species: *Taeniostola celophora* Meyrick, 1920b:327, by original designation. Type locality: Brazil: Rio Trombetas [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic] as a replacement name for *Taeniostola* Meyrick, 1920.

Taleporia Hübner, [1825]:400

Psychidae

Type-species: *Tinea pseudobombycella* Hübner, 1796:pl. 31, fig. 212, by subsequent designation of Fletcher (1929:215). Type locality: [Europe] [type lost?].

Originally described in Tineae; subsequently considered in Glyphipterygidae [sic] by Meyrick (1912b:123); currently in Psychidae.

Tebenna Billberg, 1820:90

Choreutidae

Type-species: *Tinea bjerkanndrella* Thunberg, 1784:24, by subsequent designation of Bradley (1966b:220). Type locality: Sweden [type, Univ. Uppsala].

Originally described in Tortrices; subsequently transferred to Glyphipterigidae by Bradley (1966b:220); transferred to Choreutidae by Heppner (1977b:632).

Tebenna Hübner, [1825]:414

Agonoxenidae

Type-species: *Tinea festivella* [Denis and Schiffermüller], 1775:319, by subsequent designation of Fletcher (1929:216). Type locality: [Austria]: Vienna [type lost?].

Originally described in Tineae Incertae; now a junior subjective synonym of *Heinemannia* Wocke, 1853, in Agonoxenidae: Blastodacninae.

Tebenna Hübner, [1825], is a junior homonym of *Tebenna* Billberg, 1820 (Choreutidae).

Tebeuna [sic] Danilevsky, 1969:922 Choreutidae

A misspelling of *Tebenna* Billberg, 1820, in Choreutidae.

Tegna Walker, 1866:1809 Brachodidae

Type-species: *Tegna hyblaeella* Walker, 1866:1810 [= *Chimaera radiata* Ochsenheimer, 1808:5], by monotypy. Type locality (*hyblaeella*): Nepal [lectotype unselected, BMNH].

Originally described in Choreutidae; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Phycodes* Guenée, 1852, by Meyrick (1913b:32); transferred to Brachodidae by Heppner (1981a:14) as a junior subjective synonym of *Phycodes* Guenée, 1852.

Tetracmanthes Meyrick, 1925a:136 Glyphipterigidae

Type-species: *Tetracmanthes astrocosma* Meyrick, 1925a:136, by monotypy. Type locality: [South Africa]: Weenan, Natal [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic].

Tharmatographa [sic] Diakonoff, 1977b:51 Tortricidae

A misspelling of *Thaumatographa* Walsingham, 1897, now in the tribe Hilarographini of Tortricidae: Chlidanotinae.

Thaumatographa Walsingham, 1897:52 Tortricidae

Type-species: *Hilarographa zapyra* Meyrick, 1886:286, by original designation. Type locality: [Papua]: Port Moresby, New Guinea [holotype ♂, BMNH].

Originally described in Glyphipteryginae [sic] of Hyponomeutidae [sic]; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Hilarographa* Zeller, 1877, by Meyrick (1913b:24) transferred to the tribe Hilarographini of Tortricidae: Chlidanotinae by Diakonoff (1977b:22).

Thaumatotibia Zacher, 1915:529 Tortricidae

Type-species: *Thaumatotibia roerigii* Zacher, 1915:529 [= *Argyroplote leucotreta* Meyrick, 1913], by monotypy. Type locality (*roerigii*): Togo: Sokodé, Bassari [type lost?].

Originally described without family placement; subsequently transferred to Tortricidae: Olethreutinae by Heppner (1980:334), as a junior subjective synonym of *Cryptophlebia* Walsingham, 1899.

Thelethia Dyar, 1893:301 Incurvariidae

Type-species: *Thia extranea* H. Edwards, 1888:181, by original designation. Type locality: USA: Los Angeles, California [lectotype ♂ (Davis, 1967:44), INHS].

Originally described in Tineidae as a replacement name for *Thia* H. Edwards, 1888; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:29); transferred to Incurvariidae as a junior subjective synonym of *Tegeticula* Zeller, 1873, by Davis (1967:29).

Thia H. Edwards, 1888:181

Incurvariidae

Type-species: *Thia extranea* H. Edwards, 1888:181, by monotypy. Type locality: USA: Los Angeles, California [lectotype ♂ (Davis, 1967:44), INHS].

Originally described in Heterogynidae; subsequently transferred to Glyphipterygidae [sic] in synonymy with *Thelethia* Dyar, 1893, by Meyrick (1913b:29); transferred to Incurvariidae as a junior subjective synonym of *Tegeticula* Zeller, 1873, by Davis (1967:29).

Thia H. Edwards, 1888, is a junior homonym of *Thia* Leach, 1815 (Crustacea), *Thia* Oken, 1815 (Polychaeta), and *Thia* Newman, 1840 (Coleoptera).

Thrasydoxa Meyrick, 1912a:60

Heliodinidae

Type-species: *Thrasydoxa tyrocopa* Meyrick, 1912a:60, by monotypy. Type locality: Colombia: San Antonio [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Heliodinidae by Meyrick (1913b:18).

Thriambeutis Meyrick, 1910:470

Heliodinidae

Type-species: *Thriambeutis hemicausta* Meyrick, 1910:470, by monotypy. Type locality: Solomon Is.: Isabel Id. [holotype ♀, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Heliodinidae by Meyrick (1913b:19).

Thylacopleura Meyrick, 1886:284

*Immidae

Type-species: *Thylacopleura autodoxa* Meyrick, 1886:285, by monotypy. Type locality: Fiji [lectotype unselected, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred as a synonym of *Imma* Walker, [1859], to Plutellidae by Meyrick (1906c:170); hereby transferred to Immidae as a junior subjective synonym of *Imma* Walker, [1859].

Tinagma Zeller, 1839:203

Douglasiidae

Type-species: *Tinagma perdicellum* Zeller, 1839:204, by subsequent designation of Fletcher (1929:223). Type locality: [Germany]: Spitzberg [lectotype unselected, BMNH].

Originally described in Tineana; subsequently transferred to Glyphipterygidae [sic] by Stainton (1854:178); transferred to Douglasiidae by Meyrick (1928:721).

Topaza Walker, 1864:808

*Immidae

Type-species: *Topaza alienella* Walker, 1864:808, by monotypy. Type locality: [Malaysia]: Sarawak [holotype ♂, BMNH].

Originally described in Gelechiidae [sic]; subsequently transferred as a synonym of *Imma* Walker, [1859], to Plutellidae by Meyrick (1906c:170) and to Glyphipterygidae [sic] by Meyrick (1913b:25); hereby transferred to Immidae as a junior subjective synonym of *Imma* Walker, [1859].

Tortricomorpha C. Felder, 1861:34

*Immidae

Type-species: *Tortricomorpha atosignata* C. Felder, 1861:35, by subsequent designation of Meyrick (1906c:170). Type locality: [Indonesia]: Amboina, [Moluccas Is.] [holotype ♀, BMNH].

Originally described in Arctiidae; subsequently transferred to Atychiidae [sic] [=Brachodidae] by Lower (1903:69); transferred to Plutellidae by Meyrick (1905:611); transferred to Glyphipterygidae [sic] as a synonym of *Imma* Walker, [1859], by Meyrick (1913b:25); hereby transferred to Immidae as a junior subjective synonym of *Imma* Walker, [1859].

Tortyra Walker, 1863:510

Choreutidae

Type-species: *Tortyra spectabilis* Walker, 1863:510, by subsequent designation of Busck (1914:57). Type locality: Brazil: Ega [=Tefé] [lectotype ♂ (present designation), BMNH].

Originally described in Tineidae; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1910:462); transferred to Choreutidae by Heppner (1977b:633).

Trapeziophora Walsingham, 1892:529

Glyphipterigidae

Type-species: *Trapeziophora gemmula* Walsingham, 1892:530, by original designation. Type locality: St. Vincent [lectotype ♂ (present designation), BMNH].

Originally described in Glyphipteryginae [sic] of Tineidae; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:40) as a synonym of *Ussara* Walker, 1864; here considered a distinct genus.

Trichothyrsa Meyrick, 1912a:61

Heliodinidae

Type-species: *Trichothyrsa flammivola* Meyrick, 1912a:61, by original designation. Type locality: India: Coorg [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred to Heliodinidae by Meyrick (1913b:19).

Tyriomorpha Meyrick, 1918:191

Oecophoridae

Type-species: *Cryptolechia phoenissa* Butler, 1883:81, by original designation. Type locality: Chile: Corral [holotype ♂, BMNH].

Originally described in Glyphipterygidae [sic]; subsequently transferred

to Oecophoridae as *Mattea* Duckworth, 1966, a junior objective synonym of *Tyriomorpha* Meyrick, 1918; Clarke (1979:142) transferred *Tyriomorpha* to Oecophoridae: Oecophorinae, now a junior subjective synonym of *Pachyphoenix* Butler, 1883, **new synonymy** (Becker, pers. comm.).

Usara [sic] Busck, [1934a]:182 Glyphipterigidae
A misspelling of *Ussara* Walker, 1864.

Ussara Walker, 1864:800 Glyphipterigidae
Type-species: *Ussara decoratella* Walker, 1864:801, by monotypy. Type locality: Brazil: Ega [=Tefé] [holotype ♀, BMNH].

Originally described in Gelechiidae [sic]; subsequently transferred to Glyphipterygidae [sic] by Meyrick (1913b:40).

Vinzela Walker, [1866]:1260 *Immidae
Type-species: *Vinzela inaptalis* Walker, [1866]:1261, by monotypy. Type locality: [Malaysia]: Sarawak [holotype ♂, UMO].

Originally described in Pyralidae; subsequently transferred to Gelechiidae [sic] as a synonym of *Tortricomorpha* C. Felder, 1861, by Walsingham (1900a:78); transferred as a synonym of *Imma* Walker, [1859], to Plutellidae by Meyrick (1906c:170) and to Glyphipterygidae [sic] by Meyrick (1913b:25); hereby transferred to Immidae as a junior subjective synonym of *Imma* Walker, [1859].

Walsinghamia Riley, 1889:157 Choreutidae
Type-species: *Walsinghamia diva* Riley, 1889:158, by monotypy. Type locality: USA: Cocoanut Grove, [Miami], Florida [lectotype ♀ (present designation), USNM].

Originally described in Noctuidae; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Tortyra* Walker, 1863, by Meyrick (1913b:33); transferred to Choreutidae as a junior subjective synonym of *Hemerophila* Hübner, [1817], by Heppner (1977b:634).

Xylopoda Latreille, 1829:412 Choreutidae
Type-species: *Tortrix dentana* Hübner, [1796–99]:pl. 1, fig. 4 [= *Phalaena* (*Tortrix*) *fabriciana* Linnaeus, 1767:880], by monotypy. Type locality (*dentana*): [Europe] [type lost?].

Originally described in Tortrices; subsequently transferred to Glyphipterygidae [sic] as a synonym of *Simaethis* Leach, 1815, by Meyrick (1913b:34); transferred to Choreutidae as a junior subjective synonym of *Anthophila* Haworth, [1811], by Heppner (1981a:50).

Xylopoda Latreille, 1829, is a junior homonym of *Xylopoda* Berthold, 1827.

Xylopoda Berthold, 1827:484 Choreutidae
Type-species: *Tortrix dentana* Hübner, [1796–99]:pl. 1, fig. 4 [= *Pha-*

laena (*Tortrix*) *fabriciana* Linnaeus, 1767:880], by monotypy. Type locality (*dentana*): [Europe] [type lost?].

Originally described in Tortrices; subsequently forgotten in lieu of *Xylopoda* Latreille, 1829, in Glyphipterygidae [sic] and as a synonym of *Simaethis* Leach, 1815, by Meyrick (1913b:34); now a junior subjective synonym of *Anthophila* Haworth, [1811].

Xylopoda Berthold, 1827, was published ahead of Latreille (1829) in a German edition of Latreille's work, with additions by Berthold.

Xylopode Latreille, 1825:476 Choreutidae

A vernacular spelling, later corrected to *Xylopoda* Latreille, 1829; now an invalid name under *Anthophila* Haworth, [1811].

Xylopodo [sic] Morris, 1872:iv Choreutidae

A misspelling of *Xylopoda* Latreille, 1829 [= *Xylopoda* Berthold, 1827], now a junior subjective synonym of *Anthophila* Haworth, [1811], in Choreutidae.

Zodia Heppner, 1979b:685 Choreutidae

Type-species: *Simaethis plutusana* Walker, 1863:453, by original designation. Type locality: Brazil: Ega [=Tefé] [lectotype ♂ (Heppner, 1979b:689), BMNH].

Originally described in Choreutidae.

Lectotype Designations

Specimens of species listed below have been examined and are selected as lectotypes by present designation. The slash mark (/) indicates separate lines on labels; each separate label is distinguished by a semicolon. The notations "Durrant label" below indicate large black-bordered labels attached to specimens by Durrant at the British Museum (Natural History) on specimens considered the type or on syntypes.

Abrenthia cuprea Busck, 1915:87 Glyphipterygidae

Lectotype ♂ [USNM] with the following labels: Roxboro/VI. 27 Pa.; Coll. by/F. Haimbach; Type/No. 19239/U.S.N.M. [red label]; *Abrenthia/cuprea*/Type Busck; Genitalia Slide/By Heppner '76/ USNM 77247 ♂ [green label].

Paralectotypes: 2—Roxboro, Pennsylvania (1 ♂); Falls Church, Virginia (1 ♂) [USNM].

Agiton idioptila Turner, 1926a:145 Epermeniidae

Lectotype ♂ [ANIC] with the following labels (teste Common): National Pk., Q., 47, 1-1-21; *Agiton idioptila* Turn./TYPE.

Paralectotypes: 3—[Lamington] National Pk., Q[ueensland], Australia (2 ♂, 1 ♀) [ANIC].

Araeolepia subfasciella Walsingham, 1881:303 Plutellidae

Lectotype ♂ [BMNH] with the following labels: Currant Creek/Grant Co./OREGON/16. IV. 1872 Wlsm.; Walsingham/Collection/1910-427; B.M. ♂/Genitalia Slide/No. 20209.

Paralectotypes: 16—(same locality) (4 ♂, 2 ♀) [BMNH]; 2 ♂ (ex Fernald Coll.) [USNM]; 1 ♂ (ex Chambers Coll.) [MCZ]; 7 not located.

Badera pretiosa Walker, 1866:1819 Choreutidae

Lectotype ♂ [BMNH] with the following labels (teste Sattler): Type [round, red edge]; 60-15/E.I.C.; 771. [small square]; Type ♂ [Durrant label]. [abdomen missing].

Paralectotypes: 1 ♂—Java [BMNH].

Callizyga dispar Turner, 1894:132 Oecophoridae

Lectotype ♂ [ANIC] with the following labels (teste Common): Brisbane; *Callizyga dispar*/Turn./TYPE; Genitalia Slide; G463.

Paralectotypes: 1 ♀—Brisbane [Queensland, Australia] [ANIC].

Choregia fulgens Felder and Rogenhofer, 1875:6 Choreutidae

Lectotype ♂ [BMNH] with the following labels: Type [round, red edge]; 312 [small square]; Felder Coll./Rothschild/1913-86; Novara CXL/f. 17. *Choregia/fulgens* F./Bogota ♂ [Felder label]; [blank Durrant label] TYPE; FELDER'S TYPE [reversed]. [♂ abdomen glued on is incorrect one].

Paralectotypes: none [2 syntypes are from Brazil (Cuyabe [NHMV]) but belong to a different species of *Tortyra*].

Circica cionophora Meyrick, 1888:88 Glyphipterigidae

Lectotype ♂ [BMNH] with the following labels: Christchurch/New Zealand/24-II-1882/Meyrick 1888/1740; Walsingham/Collection/1910-427; *Circica/cionophora* Meyr./Named by Meyrick; B.M. ♂/Genitalia Slide/No. 20236.

Paralectotypes: 12—(same locality, 24.2.82) (11 ♂, 1 ♀) [BMNH].

Ditrigonophora marmoriepennis Walsingham, 1897:118 Yponomeutidae

Lectotype [sex unknown] [BMNH] with the following labels: Balthazar/Grenada.

Paralectotypes: 1 [BMNH]. [Both syntypes are without heads or abdomens.]

Epithetica typhoscia Turner, 1923:165 Oecophoridae

Lectotype ♂ [ANIC] with the following labels (teste Common): Lismore, N.S.W./22-10-22; *Epithetica/typhoscia* Turn./TYPE.

Paralectotypes: 1 ♂—(same locality and date) [ANIC].

Euprophantis autoglypta Meyrick, 1921a:191 Gracillariidae

Lectotype ♂ [RMNL] with the following labels (teste Diakonoff): Java/

Pekalongan/v. Deventer; Coll. Piepers/Snellen, Java; [genitalia mini-slides] 2122 & 2122a; Type [red label].

Paralectotypes: 2 (same locality) [specimens not located].

Idiothauma africanum Walsingham, 1897:49 Tortricidae

Lectotype ♂ [BMNH] with the following labels: Type [round, red' edge]; Kangwé/Ogowé River/FRENCH CONGO/Good-Holland, 6967; Walsingham/Collection/1910-427; [Durrant label] TYPE ♂; B.M. ♂/Genitalia Slide/No. 20233.

Paralectotypes: 2—(same locality) [specimens not located; not at BMNH].

Melanoxena falsissima Dognin, 1910:121 Choreutidae

Lectotype ♂ [USNM] with the following labels: Colombie/Fassel; *Melanoxena/falsissima*/Dgn./type ♂; Durrant/12.6.12; 6554/Wlsm. 1911; "8/4.08 S. Antonio" [folded]; (*Melanoxena*)/gen. nov./(*falsissima*)/sp. nov./Warren 1.7.09; Dognin/Collection; Type No. /32355/U.S.N.M. [red label].

Paralectotypes: 2♂—(same locality) [USNM].

Pantosperma holochalca Meyrick, 1888:89 Glyphipterigidae

Lectotype ♂ [BMNH] with the following labels: Makotaku/ N. Zealand/ 8-III-1883/Meyrick 1888, 1691; Walsingham/Collection/1910-427; *Pantosperma/holochalca* Meyr./Named by Meyrick; B.M. ♂/ Genitalia Slide/No. 20238.

Paralectotypes: 11—(same locality) 10 ♂, 1 ♀ [BMNH].

Sciaphila trigonana Walsingham, 1879:22 Copromorphidae

Lectotype ♀ [BMNH] with the following labels: N. nr. Mendocino City/ CALIFORNIA/3-5 VI. 1871/Wlsm. 91861; Brit. Mus./1880-75; [Durrant label] TYPE ♂ [sic]; B.M. ♀/Genitalia Slide/No. 20212.

Paralectotypes: 5—(same locality) 1 ♂, 4 ♀ [BMNH].

Simaethis pronubana Snellen, 1877:48 Choreutidae

Lectotype ♀ [RMNL] with the following labels (teste Diakonoff): Java [in Pieper's handwriting] [abdomen missing].

Paralectotypes: 4—(same locality) [specimens not located; not at RMNL].

Sphinx appendiculata Esper, 1783:227 Brachodidae

Lectotype ♀ [SMW] with the following labels: [no data; Coll. Gerning].

Paralectotypes: 3 ♀—[no data; Coll. Gerning]. (The Gerning Collection dates from the late 1700's to early 1800's and contains the remaining Esper types.)

Tortyra spectabilis Walker, 1863:510 Choreutidae

Lectotype ♂ [BMNH] with the following labels: Ega/57, 125 [reverse] [blue, round label]; [Durrant label] *Tortyra spectabilis* Wkr./"28/510 e"/ PARATYPE "5/6"; B.M. ♂/Genitalia Slide/No. 20223.

Paralectotypes: 3 ♂—(same locality [Tefé, Amazonas, Brazil]) [BMNH].
[Two other syntypes belong to another species of *Tortyra*.]

Trapeziophora gemmula Walsingham, 1892:530 Glyphipterigidae

Lectotype ♂ [BMNH] with the following labels: Type H.T. [round, red edge]; St. Vincent, W.I./H.H. Smith; Walsingham/Collection/1910-427/65356; [Durrant label] TYPE ♀ [sic]; B.M. ♂/Genitalia Slide/No. 20235.

Paralectotypes: 1 ♂—“Windward side/St. Vincent, W.I./H.H. Smith”; (Walsingham Coll. 65355) [BMNH].

Walsinghamia diva Riley, 1889:158 Choreutidae

Lectotype ♀ [USNM] with the following labels: Type/No. 400/U.S.N.M. [red]; Walsinghamia/diva/Type Riley. [abdomen missing].

Paralectotypes: 2—(same locality) [Cocoanut [sic] Grove, Florida], (1 ♂, 1 ♀) [USNM].

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Department of Entomology, Smithsonian Institution, Washington, D.C.
20560.

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denticulella (Thunberg), *Callisto*
diana (Hübner), *Allononyma*
diana (Hübner), *Hemerophila*
diana (Hübner), *Orchemia*
dichroalis Snellen, *Bursadella*
dispar Turner, *Callizga*
diva Riley, *Walsinghamia*
divitiosa Walker, *Saptha*
dolopis Durrant, *Cibdeloses*
dolosana (Herrich-Schäffer), *Millieria*
dolosana (Herrich-Schäffer) *Ripismia*
drosophaes Meyrick, *Phyrganostola*
editha Busck, *Ellabella*
electrodes Diakonoff, *Cercosimma*
encomias Meyrick, *Symphorostola*
eratopis Meyrick, *Protosynaema*
erxlebelli (Fabricius), *Roeslerstammia*
extraenea (H. Edwards), *Thelethia*
extraenea H. Edwards, *Thia*
fabriciana (Linnaeus), *Anthophila*
fabriciana (Linnaeus), *Simaethis*
fabriciana (Linnaeus), *Xylopoda*
fabricii Haworth, *Anthophila*
falsissima Dognin, *Melanoxena*
fervescens Meyrick, *Amphiclada*

festivella (D. & S.), *Tebenna fibrana* Hübner, *Porpe flammivola* Meyrick, *Trichothyrsa flaviceps* (F. & R.), *Setiostoma forsterella* (Fabricius), *Heribeia friserella* Busck, *Ordrupia fueslella* (Fabricius), *Aechmia fulgens* (Erschoff), *Desmidoloma fulgens* F. & R., *Choregia funebris* (Feisthabel), *Brachodes fyeslella* [sic] (Fabricius), *Aechmia gallicana* Guenée, *Orchemia gaurisana* Walker, *Rhobonda gemmula* Walsingham, *Trapeziophora granulata* Meyrick, *Cronicombra guttea* (Haworth), *Callisto gyrtioniformis* Hampson, *Sthenistis halticella* Eaton, *Embryonopsis harpodes* Meyrick, *Picrodoxa hemicamina* Meyrick, *Sisyroctenis hemicausta* Meyrick, *Thriambeutis hemichryseis* Hampson, *Scaptesylix heptachalca* Meyrick, *Hoplophractis hesperialis* Walker, *Dudua hirurginicornis* Guenée, *Phycodes holochalca* Meyrick, *Pantosperma hubneriana* (Stoll), *Mictopsichia hyblaeella* Walker, *Tegna ichthyopa* Meyrick, *Iridostoma idiopitila* Turner, *Agiton impigritella* (Clemens), *Diploschizia inaptalis* Walker, *Vinzela incisalis* (Treitschke), *Macropia innotabilis* Walker, *Plotheia iophanes* Meyrick, *Hierodoris iridesma* Meyrick, *Carmentina iridoxa* (Meyrick), *Charixena iridoxa* Meyrick, *Philpottia iridozona* Meyrick, *Aeolocosma irina* Meyrick, *Actinoscelis iuloptera* Meyrick, *Ereunetis japonica* (Issiki), *Litobrenthia lampronialis* Walker, *Inapha lasiochroa* Lower, *Homadaula lasiopa* Meyrick, *Colpotorna leucotelus* Walker, *Cebysa leucotelus* Walker, *Sezeris lineana* (Hübner), *Glyphipterix linneella* (Clerck), *Glyphipteryx linneella* Hübner, *Glyphipterix lutumella* Amsel, *Klimeschia*

mackwoodii Moore, *Aprata mackwoodii* Moore, *Davendra marmarastra* (Meyrick), *Nexosa marmoreipennis* Walsingham, *Ditrigonophora mathewi* Zeller, *Heliosstibes mediana* Walker, *Cotaena medinella* Staudinger, *Staintonia melanochlaena* Turner, *Aproopta melanoclista* Meyrick, *Probolacma melistoma* Meyrick, *Lasiodictis metallicella* (Duponchel), *Aechmia micaceella* Walker, *Chalenata mikadonis* (Stringer), *Charitographa myllerana* (Fabricius), *Choreutis myllerana* (Fabricius), *Prochoreutis myriospila* Meyrick, *Homadaula nemorana* (Hübner), *Entomoloma nemorana* (Hübner), *Macropia nigromaculata* (Issiki), *Mictocommosis niphadopa* Meyrick, *Ptochaula obscurepunctella* (Stainton), *Perittia ocnerostomellum* (Stainton), *Douglasia oligodrachma* Diakonoff, *Peritropha ophideresana* Walker, *Orosana pachypus* Diakonoff, *Polygiton palaeodes* (Meyrick), *Alampla pariana* (Clerck), *Choreutis pariana* (Clerck), *Eutromula pariana* (Clerck), *Hemerophila pavonacella* Clemens, *Brenthia percussana* (Walker), *Allotropha perdicellum* Zeller, *Tinagma perornatella* (Walker), *Desmidoloma perornatella* (Walker), *Lepidotarphius phoenissa* (Butler), *Mattea phoenissa* (Butler), *Tyriomorpha planipes* Diakonoff, *Ganabalia plumbigera* Meyrick, *Encratora plutostola* Diakonoff, *Embolostoma plutusana* (Walker), *Zodia pretiosa* Walker, *Badera pronubana* (Snellen), *Chordates pseudobombycella* (Hübner), *Taleporia punctatella* (Walker), *Carna punctatella* Walker, *Rhobonda punctigera* Rebel, *Paraprays purpurascens* Hampson, *Callartona purpurata* Meyrick, *Lamprystica purpurina* (D. & S.), *Anthophila purpurina* (D. & S.), *Anthophilae pygmaeodes* Turner, *Nesotropha*

pygmeana (Haworth), *Acrolepia*
pyractis Meyrick, *Archimaga*
radiata Ochsenheimer, *Chimaera*
radiata (Ochsenheimer), *Phycodes*
radiata (Ochsenheimer), *Tegna*
resumptana Walker, *Miscera*
robusta Walker, *Sagalassa*
roerigii Zacher, *Thaumatotibia*
rugosalis Walker, *Imma*
saldonana (Fabricius), *Procerata*
sanguinea Butler, *Pachyphoenix*
sapphiropa Meyrick, *Irianassa*
satrapella Meyrick, *Eupselia*
saturata (Walker), *Methypsa*
semilinea Walker, *Jobula*
sepias Meyrick, *Loxotrochis*
sexfasciella Sauber, *Choreutidia*
silvana Meyrick, *Bryonympha*
simpliciella (Stephens), *Anacampsoides*
soldana [sic] Berthold, *Procerata*
spectabilis Walker, *Tortyra*
spiraea Heppner, *Neomachlotica*
splendens Pryer, *Lepidotarphius*
sporimaea Meyrick, *Lygronoma*
sporomantis Meyrick, *Rhabdocrates*
statices (Linnaeus), *Atychia*

stella Meyrick, *Coridomorpha*
subfasciella Walsingham, *Araeolepia*
succedanea Walsingham, *Philodoria*
swederiana (Stoll), *Hilarographa*
tenebrifera Turner, *Mylocera*
thesaurella Meyrick, *Hypertropha*
thiolychna Meyrick, *Electrographa*
thrasonella (Scopoli), *Aechmia*
tinthalea (Meyrick), *Amphimelas*
trigonana (Walsingham), *Lotisma*
typhoscia Turner, *Epithetica*
tyrocopa Meyrick, *Thrasydoxa*
vacua (Walker), *Sesiomorpha*
valida (Walker), *Jonaca*
velutina Walker, *Moca*
vernetella Guenée, *Brachodes*
vexatalis Walker, *Alicadra*
vibrana (Hübner), *Porpe*
vicarialis Zeller, *Hemerophila*
xanthobasis Zeller, *Setiostoma*
xanthoplaca Turner, *Euthorybeta*
xanthoprocta (Meyrick), *Atractoceros*
xylophragma Meyrick, *Antispastis*
zapyra Meyrick, *Hilarographa*
zapyra (Meyrick), *Thaumatographa*

STUDIES OF NORTH AMERICAN *ERORA* (SCUDDER)
(LEPIDOPTERA, LYCAENIDAE)

Alexander B. Klots¹ and Cyril F. dos Passos²

Abstract.—The genus *Erora* Scudder is characterized and discussed. Characteristics of *E. laeta* (Edwards), *E. quaderna quaderna* (Hewitson) and *E. quaderna sanfordi* dos Passos are given and evaluated. The early stages, ethology, ecology and geographic distributions of *E. laeta* and *E. quaderna sanfordi* are described. The peculiar dense vestiture of the larvae, and a “bald” area (the calvarium) on the prothorax, are potentially significant in generic taxonomy. Full, annotated synonymies and lists of distributional records are given. Possible phylogenies are discussed.

Introduction

For many years the authors pursued studies of the North American *Erora*, first of *E. laeta* and more recently of *E. quaderna sanfordi*. The work has consisted of three main parts: field studies of the life histories, ecology and ethology; compilations of records and data from museum specimens, the published literature and personal communications; and comparative taxonomic studies. This article deals with these taxa in North America north of Mexico; but it also contains some notes and comments on the still little-known *E. q. quaderna* and *E. caudata* Miller in Mexico.

Acknowledgments

We are greatly indebted to many persons for information and assistance. From John H. Cook, A. C. Frederick and James Sanford we learned about the two localities in Vermont where most of our eastern field studies were made. The late Sidney Hessel furnished notes and records, and generously refrained from collecting in the areas where we were doing life-history work. (What greater sacrifice can a devoted collector make?) Joseph J. Copeland checked many plant identifications. T. G. Howarth of the British Museum (Natural History) picked out and dissected for our study the types of *E. attalion* (Godman and Salvin), *E. quaderna* (Hewitson) and possibly related species. W. D. Field of the U.S. National Museum gave us many data about genitalic structures and neotropical species. Harry Clench of the Carnegie

¹ Research Associate, American Museum of Natural History.

² Research Associate, American Museum of Natural History and Carnegie Museum.

Museum very kindly gave us transcripts of his and Lee D. Miller's field data on *E. quaderna* in Mexico, and data on the differentiation of *E. q. quaderna* and *E. q. sanfordi*. A. C. Allyn, Director and Lee D. Miller, Curator, of the Allyn Museum of Entomology gave us very valuable photographic aid and sent us some needed data. Vincent Roth and Kilian Roever gave much helpful advice at the Southwestern Research Station of the American Museum of Natural History near Portal, Arizona, where *E. q. sanfordi* was studied. Numerous other individuals who have collected *E. laeta* very kindly answered our queries about the circumstances, or looked up specimens and records in collections.

Erora Scudder, 1872

4th Ann. Rept. Peabody Acad. Sci., 1871:53

Type species by original designation: *Thecla laeta* Edwards; includes also *T. clothilde* Edwards, Proc. Acad. Nat. Sci. Philadelphia, 1862 (14):55.

Erora Scudder, 1872, p. 169.

Erora Scudder, 1875, 10:166.

Erora Scudder, 1876, p. 106.

Erora Scudder, 1889, 2:815.

Erora Scudder, Dyar, "1902" [1903], p. 40.

Erora Scudder, Barnes and Benjamin, 1926, p. 18.

Erora Scudder, McDunnough, 1938, p. 25.

Erora Scudder, Procter, 1938, p. 186.

Erora Scudder, Field, 1941, p. 303.

Erora Scudder, dos Passos, 1964, p. 55.

Erora Scudder, Hemming, 1967, p. 169.

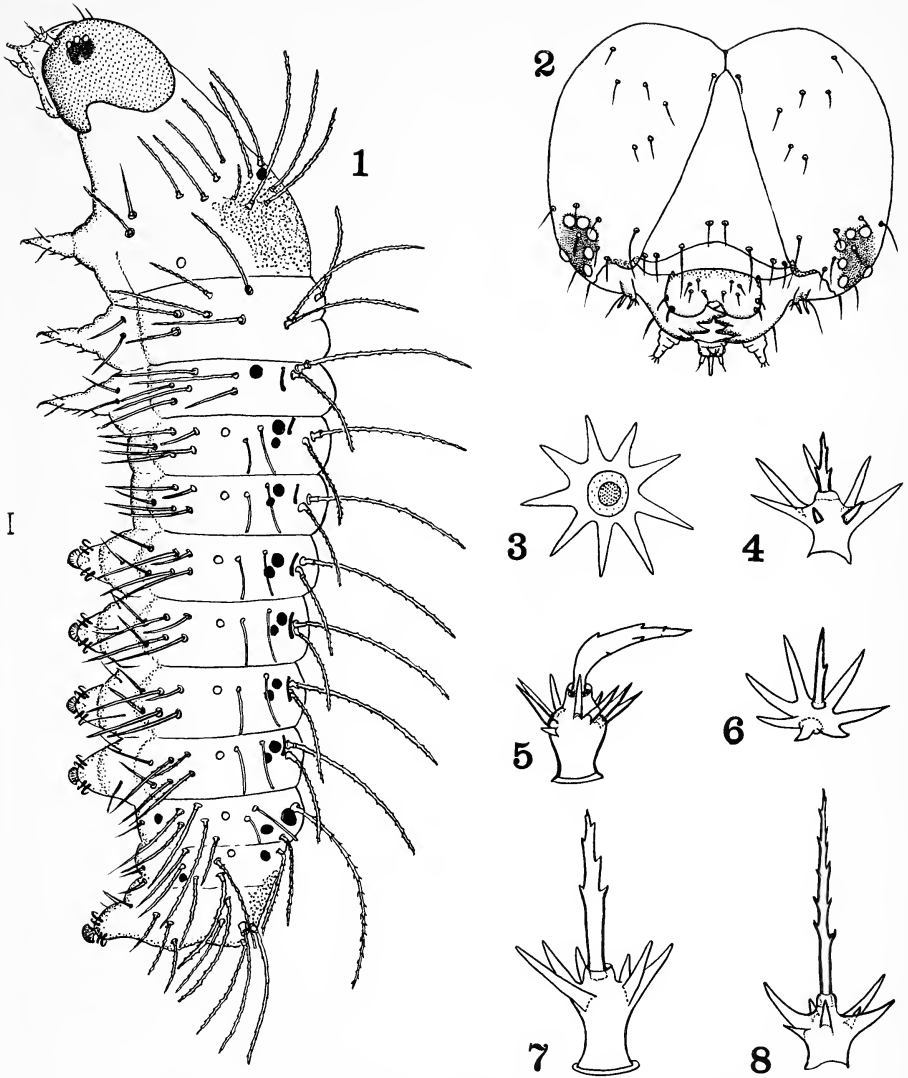
Erora Scudder, dos Passos, 1970, p. 35.

Erora Scudder, Miller, 1980, p. 209.

Field (1941) added *Thecla quaderna* Hewitson, 1868 to *Erora* so that the genus consisted of two species, *laeta* and *quaderna*; in 1980 Miller added *E. caudata*.

Scudder's original description of *Erora* read as follows: "Lower Canada to Virginia. Head moderately large; front as broad as the eyes on a front view and scarcely half as high again as broad; eyes thinly pilose; palpi slender, but little longer than the eye. Fore tibiae about four-fifths the length of the hind tibiae; middle and hind tibiae of about equal length; first superior branch of the subcostal nervure [R_1] arising, at least in the female, a very little beyond the middle of the upper border of the cell; the second [R_2] about midway between this and apex, cell slightly more than half as long as the wing."

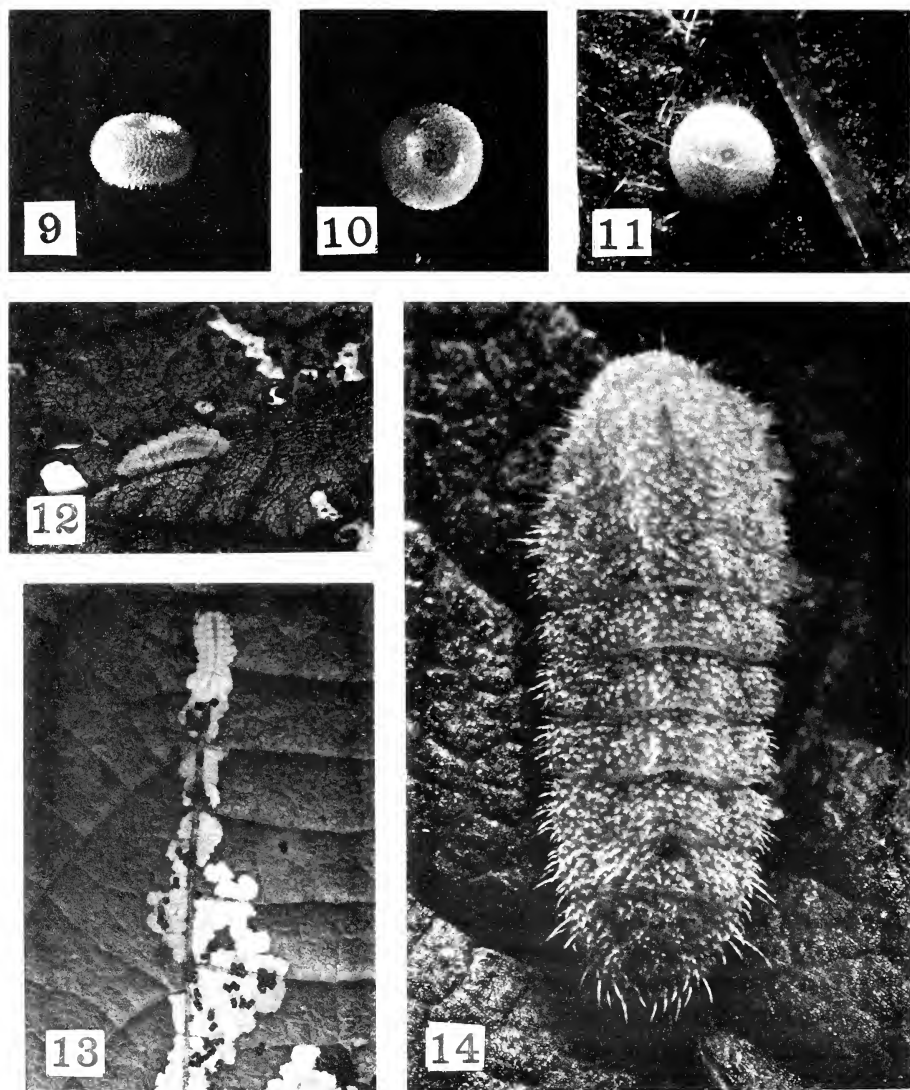
To Scudder's original characterization we add the following, based on



Figs. 1-8. *Erora laeta*. 1. 1st instar larva, left lateral view. 2. 2nd instar larva, cephalic view, head. 3-8. 5th instar larvae, coronate chalazae.

both *laeta* and *quaderna*, and on the characters given by Miller for *caudata*. Very likely some of the characters cited will prove of secondary importance when more is known about the neotropical Theclini.

Male wings lacking stigma or scent pad: Both sexes of *laeta* and *quaderna* with outer margin of hindwing even, with no tails, anal projections or lobes;



Figs. 9-14. *Erora laeta*. 9. Egg, lateral view. 10. Same egg, terminal view. 11. A different egg, terminal view. 12. 2nd instar larva, lateral view. 13. The same larva, dorsal view, showing characteristic skeletonizing of leaf. 14. 3rd instar larva, dorsal view, disproportionately greatly enlarged.

caudata with a short tail at CU_2 . Wings deep fuscous above with some iridescent blue in male, much more in female. Hindwings and at least apical area of forewings beneath pigmented green with transverse rows of spots; these, and to some degree fringes, orange to orange-red.

Male genitalia with labides broad and rounded: A longitudinal sclerotized strip in fultura superior. Falces strongly curved and pointed, wholly well separated from each other. Tegumen with no processes from ventro-caudal angle. Valvae well separated from each other, broad basally, terminally bent strongly dorsad and pointed, terminal margins not toothed. Aedeagus long and thick, its basal opening nearly half the length of the penis; penis with a short terminal spine. Cornutus normally well basad in penis, thick, basally blunt, tapering to a point, about $\frac{1}{3}$ the length of penis.

Female genitalia with papillae anales long, slender, setose: A single pair of apophyses (apophyses posteriores) bluntly angled or curved ventrad, caudad of middle. Ostium bursae well sclerotized, flat, its dorsal wall (lamella postvaginalis) split and extending farther caudad than its ventral wall (lamella antevaginalis), subterminally widened and then tapering caudad to a blunt, rounded end. Ductus bursae short, wide, containing a well sclerotized, doubled structure with a median series of short, transverse grooves; ductus seminalis coming off dorso-caudally from this, bending laterad. Bursa copulatrix elongate, with a pair of sclerotized signa, each an oval plate with a longitudinal, projecting keel tapering gradually cephalad to a fine, single or double point. Field (1951) gives excellent figures of the genitalia of *laeta* and *quaderna*, and Miller (1980) of *caudata*, which we do not think it necessary to duplicate.

Egg (*laeta* only, Figs. 9–11): Not strongly flattened, laterally rounded, with a great many short, very fine, conical projections arising from the junctions of very fine, raised ridges.

Larva, mature (*laeta* and *sanfordi*): Light greenish, patterned with dark reddish spots (*laeta*) or unmarked (*sanfordi*). Very thickly covered with various sizes of coronate chalazae, each bearing a single terminal, very finely spiculate seta (Figs. 3–8). Prothorax with a median dorsal, diamond-shaped, or scutelliform, area of very minute vestiture which we term a "calvarium" (Latin—*calvus*, bald). Prominent dorsolateral and ventrolateral ridges, the areas between these slightly concave. Swellings in each segment along dorsolateral ridges give the larva a somewhat serrate aspect in lateral profile. A pair of more prominent swellings on mesothorax. No honey gland or associated tubercles. No silk girdle seen (three larvae pupated in captivity): cremasteral pads and bristles normal.

Pupa (two of *laeta*, one of *sanfordi*): Short, rounded, with darker and lighter areas caused by the relative amount of sclerotization in the irregular meshwork of ridges. Vestiture sparse, of single, minutely spiculate setae; no complex projecting chalazae. Stridulatory organ with the grating surface heavily sclerotized, of many short, fine, parallel, almost uniform ridges.

Foodplants: Fagaceae (*Fagus* and *Quercus*) as far as known; perhaps also Corylaceae (*Corylus*).

Phylogeny: For phylogenetic speculations we are concerned here with

only *laeta* and *sanfordi*, omitting *caudata*. Obviously *laeta* and *sanfordi* are very closely related to each other, yet the wide separation of their geographic ranges presents something of a problem. *E. laeta* occurs from southern Canada southward to Virginia, Tennessee, Kentucky and Georgia along the Appalachian highlands. If considered alone it might well be judged a species of Nearctic origin with southward extensions along the mountains, as is the case with many northern species. *E. quaderna quaderna*, on the other hand, occurs from south-central Mexico southward to Guatemala and Costa Rica, but has an isolated subspecies (*sanfordi*) in the southern Rocky Mountains and northern Mexico. This distribution is characteristic of many neotropical species. Attempting to reconcile the close relationship of the two species with their very different distributions, we see two possibilities:

(1). *Erora* may have evolved as an oak-feeding *quaderna*-like stock in the central or southern Mexican highlands. Then, as a Pleistocene glaciation (probably the Wisconsin) pushed the biota southward, the northern beech-birch-maple forest reached this region. Most of the *quaderna*-like population would be forced farther southward along the Central American Cordillera; but some of it, lagging behind, became adapted to a beech-feeding life in the deciduous (and less xeric) forest, and evolved changes that led to *laeta*. Then as the glaciation subsided this differentiating *laeta* accompanied the boreal forest northward to its present northern range. Meanwhile, the southern *quaderna*-like stock evolved into the present *quaderna* (and perhaps other species) and moved northward in Mexico again, and along the Sierra Madre Occidental (and perhaps the Sierra Madre Oriental) into the southern Rocky Mountains of New Mexico and Arizona along with the "live-oaks." After this, we know, followed a period of climatic desiccation (which still continues) that formed the Sonoran and Chihuahuan deserts. This pinched off the northern population, which evolved into *E. quaderna sanfordi*, separated by desert from *E. q. quaderna* and by the arid Great Plains from *E. laeta*.

(2). A second possibility is that *Erora* may have originally evolved as a *laeta*-like stock in the northern deciduous forest. During the Wisconsin glaciation this would have been pushed far southward into Mexico. On the recession of the glacier this population would have returned northward as *laeta*. Left behind in Mexico were populations that evolved there into the live-oak feeding *quaderna*; and from these, as postulated above, evolved the northern isolate, *E. quaderna sanfordi*.

We consider the first of these alternatives to be the more likely, chiefly because of the existence in Mexico and southward of other species (e.g. *E. caudata* Miller) very similar to, and possibly congeneric with, *quaderna*; and also because of the differentiation of *quaderna* into two subspecies, while the more recently evolved *laeta* has remained homogeneous. Cer-

tainly a great deal more fieldwork and collecting is needed along the Sierra Madre Occidental, Sierra Madre Oriental and Sierra Madre Transversal, and also southward along the highlands of Central America, to learn both more about *quaderna* itself, and also more about the possible other *Erora* and *Erora*-like species in this region. *E. caudata* was named "from cloud forest," and there may be yet-undescribed species in this environment; while undescribed species of a *quaderna* stock may exist in the more xeric highlands of southern Mexico and southward.

Erora laeta (Edwards) ♂, 1862

Erora clothilde (Edwards) ♀, 1863

Thecla laeta Edwards, 1863, [14] (4):55 (London, [Ontario], leg. W. Saunders) (our figures 21–22).

Thecla clothilde Edwards, 1863, 2(1):15 (Quebec, C. E., leg. Rev. M. Provancher).

Thecla laeta Edwards, Weidemeyer, "1863" [1864], 2(2):534 (British N[orth] A[merica]).

Thecla clothilde Edwards, Scudder, 1868, 11(24):377 (Streaked Mountain, near Paris, Maine, July 22, leg. Smith).

Thecla laeta Edwards, Scudder, 1868, 11(24):377 (Streaked Mountain, near Paris, Maine, July 22, leg. Smith).

Thecla laeta Edwards, "1868–72" [1869], 1(3):[139], pl. *Thecla* 1, figs. 1, 2 ♂, 3, 4 ♀ (London, [Ontario] Canada, leg. Saunders, 1861; Coalburgh, Kanawha Co., West Virginia, April 1868; Paris, Maine, July 22, leg. W. Saunders).

T[hecla] laeta Edwards, Kirby, 1871, p. 401, no. 371 (Amer. Sept.).

T[hecla] clothilde Edwards, Kirby, 1871, p. 401, no. 371 (Amer. Sept.).

Erora laeta (Edwards) (= *Thecla clothilde* Edwards), Scudder, 1872, p. 32 (lower Canada to Virginia).

Erora Scudder (1872) *laeta* (Edwards) (= *clothilde*) (Edwards), Scudder, 1876, 3(13):106, no. 203 (Ontario, Quebec and Maine [along the Appalachians?] to West Virginia).

Thecla laeta Edwards (= *clothilde* Edwards), 1877, p. 42, no. 327 (Maine to West Virginia, Ontario, Quebec).

Thecla laeta Edwards (= ♀ *Thecla clothilde* Edwards), Strecker 1878, p. 90, no. 108 (Canada, Atlantic states, Maine to Virginia).

Thecla laeta Edwards, Anon., 1881, p. 3, no. 358.

Thecla laeta Mead, 1882, 2(1):18 (Coalburgh, West Virginia, July 1881, leg. Theodore L. Mead).

Thecla laeta Edwards, Edwards (*partim*), 1883, 3(1):8 (Pr. Quebec, Ontario, Maine, Catskills, New York; White Sulphur, Coalburgh, West Virginia).

- Thecla laeta*, 1883, 3(9):123 (Coalburgh, West Virginia, April 17, 1883).
T[hecla] laeta Aaron, 1884, 4(1):22 (Sand Hills below Atlantic City, New Jersey, 1 July [1883]).
Thecla laeta Edwards, Fernald, 1884, p. 83, no. 45 (Orono, 18 May).
Thecla laeta Edwards (= ♀ *clothilde* Edwards), Edwards (*partim*), 1884, p. 299, no. 374 (Maine to West Virginia; Atlantic City, New Jersey; Ontario, Quebec).
Thecla laeta Edwards (*partim*), 1884, p. [336] (Quebec, Ontario, Maine, New York, West Virginia).
Thecla laeta Maynard, 1886, p. 37, no. 47 (Canada, Maine, West Virginia).
Thecla laeta Edwards, French (*partim*), 1886, p. 277, no. 114 (Atlantic City, New Jersey; Maine to West Virginia).
Erora laeta Scudder (*partim*), 1889, 2:819, 3: Pl. 14, figs. 6, 9; Pl. 23, fig. 2; Pl. 39, fig. 17; Pl. 55, fig. 2; Pl. 65, fig. 8 (St. Joachim 25 mi from Quebec, leg. Bowles; London, Ontario, leg. Saunders; Catskills, New York, leg. Edwards; Atlantic City, New Jersey, leg. Aaron; Coalburgh, Kanawha Co., West Virginia, leg. Edwards; Streaked Mt. near Paris, leg. Smith; Orono, Maine, leg. Fernald; Graylock Hopper, Williamstown, Massachusetts, leg. Scudder).
Thecla laeta Edwards, Winn, 1891, 23(5):96 (Beloeil Mt. 22 mi east Montreal, May 24, 1888, leg. Albert F. Winn).
Thecla laeta Edwards, Maynard (*partim*), 1891, p. 37, no. 47 (Atlantic City, New Jersey).
Thecla laeta Edwards, Smith et al., 1891, p. 12, no. 296.
Thecla laeta, Maynard, 1891, p. 37, no. 47 (Canada, Maine, West Virginia).
Thecla laeta Edwards, Fyles, 1893, p. 31 (Beloeil Mt., [Quebec] May, leg. Albert F. Winn).
Thecla laeta, Scudder, 1893, p. 123 ("widely distant places").
Thecla laeta Edwards (*Erora laeta*), Bethune, 1894, p. 36, no. 56 (London and York Mills, Ontario, Beloeil Mt., St. Joachim, St. Hilaire and Quebec, May).
Thecla laeta Edwards, Fyles, 1897, p. 12 (Sherbrook, May 25, 1895, leg. Rev. Abbe Begin).
Thecla laeta Edwards (= ♀ *clothilde* Edwards), Skinner (*partim*) 1898, p. 50, no. 306 (Maine to West Virginia; Ontario, Quebec).
Thecla laeta Edwards, Holland (*partim*), 1898, p. 249, (36) pl. 29, figs. 23 ♂, 24 ♂ (Quebec to southern New Jersey westward to West Virginia).
Thecla laeta, Grant, 1898, p. 76 (cedar swamp on cedar bush near Orillia [Ontario], May 12, leg. James Walker).
Thecla laeta Edwards, Skinner, (*partim*), 1898, Synonymic Cat. N.A. Rhop., p. 50, no. 306 (Atlantic City, New Jersey).
Thecla laeta Edwards, Weed and Fiske, 1901, p. 47 (New Hampshire).

- Thecla laeta* Edwards, Smith et al., 1903, p. 7, no. 325.
- Erora laeta* (Edwards) (= *clothilde* Edwards), Dyar, "1902" [1903], p. 40, no. 383 (Montana, Colorado).
- Thecla laeta*, Young, 1904, p. 19 (Ottawa District, leg. C. H. Young).
- Erora laeta* (Edwards), Fletcher et al., 1904, p. 91, no. 383 (Meach Lake, Quebec, May 18, leg. C. H. Young).
- Thecla laeta* Edwards, Wright (*partim*), 1905, p. 62 (E[astern] states N[ew] J[ersey], Canada to Ariz[ona]).
- Thecla laeta* Edwards, Skinner, [1905], p. 18 (Maine to West Virginia; Ontario, Quebec).
- Erora laeta* (Edwards), Stevenson, 1905, p. 54 (St. Hilaire, Quebec, May 24, leg. E. C. Barwick).
- Erora laeta* (Edwards), Elrod (*partim*), 1906, p. 131 (?Montana and Colorado *fide* Dyar).
- T[hecla] laeta*, Fletcher, 1906, pp. 27, 92, no. 383 (Digby, [Nova Scotia] leg. John Russell).
- Erora laeta* (Edwards), Fletcher and Gibson, 1907, p. 119, no. 383 (Meach Lake, Quebec, June 14, 15, leg. C. H. Young).
- T[hecla] laeta* Edwards, Coolidge (*partim*), 1910, p. 374 (Quebec, S to West Virginia and W to Montana, then S to Sonora).
- Erora laeta* (Edwards), Perrin and Russell, 1912, 12:262 (Mt. Beaman, Digby, June 19, 1905, June 7, 1906, leg. Ben Lemond).
- Thecla laeta* Edwards, Winn, 1912, p. 15 (Quebec, leg. G. J. Bowles; St. Joachim, May, leg. T. W. Fyles; St. Hilaire, May, leg. Albert F. Winn; Lost River, May, leg. Lachlan Gibb; Meach Lake, leg. Charles H. Young).
- Erora Scudder laeta* (Edwards) (= ♀ *clothilde* Edwards), Barnes and McDunnough, 1917, p. 15, no. 393.
- T[hecla] laeta* Edwards (*partim*) (= ♀ *clothilde* Edwards), Draudt *in* Seitz, "1924" 1907-1924 (1920), 5:783, pl. 1044, *ibid.* 1924, pl. 1044 (eastern United States).
- Erora laeta* (Edwards), Criddle, 1922, p. 58, no. 393 (16 Island Lake, Quebec, May 18, leg. Miss Ina B. Muir) [Argenteuil Co., May 19 or 20].
- Erora laeta* (Edwards), Mousley, 1923, 55(2):26 (Hatley, Quebec, Mt. Orford, 2860, April 30, May 21, 1922 [beech]).
- Erora laeta*, Mousley, 1926, 58(12):293 (Quebec, April 1921 [beech] [ovum on *Fagus*]).
- Erora Scudder laeta* (Edwards) (= ♀ *clothilde* [Edwards]), Barnes and Benjamin, 1926, 25(1):18, no. 398.
- E[rora] laeta* (Edwards), Forbes *in* Leonard, 1928, p. 680, no. 393 (Keene Valley, Not[man]; Cortland, Wickwire, leg. Angle; Ithaca, leg. Eyer—CU; Catskill, New York, May, June, leg. Edwards).

- Thecla* (*Erora* Scudder) *laeta* (Edwards), Holland (*partim*), 1931, p. 239, no. (55), pl. 29, figs. 23 ♂, 24 ♂ underside (Quebec to southern New Jersey westward to West Virginia).
- Erora laeta* (Edwards), dos Passos and Grey, 1934, 66(8):191 (Paris, leg. Scudder; Lincoln, leg. Clayton; Mt. Desert, leg. Mrs. A. E. Brower; Maine [beech]).
- E[rora] laeta* (Edwards), Procter, "1937" [1938], p. 186 (418) (Bar Harbor, May 19, leg. Br[ower]).
- T[hecla] laeta* Edwards, Davenport and Dethier, "1937" [1938], 17(4):173 (ova, larva, food plant *Fagus*).
- Erora* Scudder *laeta* (Edwards (= ♀ *clothilde* Edwards), McDunnough, 1938, p. 25, no. 418).
- Erora laeta* (Edwards), Comstock (*partim*); 1940, 48(1):83, (Atlantic City, New Jersey, July 1, leg. Aa[ron], 2 broods, Pennsylvania, New York, New England states, eastern Canada).
- Erora laeta* (Edwards), Field, 1941, 34(2):309–311, pl. 1, fig. 1; pl. 2, figs. 1–4; pl. 3, figs. 9 and 10 (Atlantic City and Cape May, New Jersey *fide* Murray-Aaron; Huntington, West Virginia; Mt. Equinox, Manchester, Vermont, 1935; Mt. Killington, Vermont, 1937; Little River, Great Smoky Mts., Nat. Park, Tennessee, April 15, 1938, leg. Arthur Stupka; Mt. Washington, New Hampshire, leg. L. W. Sweat; London, Ontario; City of Quebec, St. Joachim, St. Hilaire, Sherbrooke, Meach Lake, 16 Island Lake, Hatley, Mt. Orford, Quebec; Digby, Nova Scotia; Paris, Bar Harbor, Lincoln, Orono, Norway, Maine; Catskill Mts., Keene Valley, Cortland, Ithaca, New York; Atlantic City, Cape May, New Jersey; Williamstown, Massachusetts; Coalburgh, West Virginia; White Sulphur, Huntington, Virginia).
- Erora laeta* (Edwards), Clench, 1943, 51(3):223 (Lake St. Joseph, Portneuf Co., Quebec, June 1932, leg. G. B. Fairchild).
- Erora laeta* Remington and Clench, 1947, 1(4):42 (Great Smoky Mts., North Carolina and Tennessee).
- Erora laeta*, Carl Cook, 1948, 2(2):22 (Crailhope, Kentucky, April 1941, May 6, 1947).
- Erora laeta* (Edwards), Klots, 1951, pp. 16, 24, pl. 16, fig. 14, pp. 129, 142 (eastern Canada, New England south to Kentucky, chiefly Canad. Zone Forest).
- Erora laeta* (Edwards), Clark and Clark, 1951, 15:85 frontispiece, fig. 8; pl. 12, a. b. (Mt. Lakes Biol. Stat., Giles Co., Virginia, June 23, 1938, leg. Lorus J. Milne).
- Erora laeta* (Edwards), Hessel, 1952, 6(1–3):34 (Cragway Spring, Mt. Washington Toll Road, New Hampshire, 4,660').
- E[rora] laeta* (Edwards), Ferguson, 1954, 23(3):197 (Mt. Beaman, leg. John

- Russell; June 19, 1905; June 2, 1908; June 7, 1906; near Digby, June 16, 1931; Armdale, May 14, 1944, leg. D. C. Ferguson).
- Erora laeta* (Edwards), Voss and Wagner, 1956, 10(1-2):20, fig. 1, 5th row; 21 (Bliss Township, Emmet Co., Michigan, May 14, 1955).
- Erora laeta* (Edwards), Lycaenidae, Clench, "1956" [1957], 10(5):161, (Powdermill Nature Reserve, 4 mi south Rector, eastern Westmoreland Co., Pennsylvania, May 3, 1956).
- Erora laeta*, Clench, 1958, p. 7 (Calverley Lodge, Powdermill Nature Reserve, Pennsylvania, May 3, 1956, leg. H. K. Clench).
- T[hecla] laeta* Edwards, Forbes, 1960, p. 131, pl. 1, fig. c (northeastern states west to Michigan, mts. of Tennessee).
- Erora laeta* Edwards, Moore, 1960, p. 17 (Bliss Township, Emmet Co., Michigan, May 14, 1955).
- Erora laeta* Edwards, Dunlop, 1960 (Algonquin Provincial Park, May 20, 1960; June 19, 1960; *Fagus* present in both places); (also records specimen in Royal Ontario Museum, Orillia, Ontario, leg. J. Walker).
- Erora laeta* (Edwards), Clench in Ehrlich and Ehrlich, [1961], p. 218, fig. 419 (Bear Mt., Vermont; south Nova Scotia, south Quebec to Appalachians to Tennessee, west to north Michigan, south-central Kentucky).
- Erora laeta* (Edwards), Smith, "1960" [1961], 14(4):239 (Benton Twp., Grafton Co., New Hampshire 1,800', June 7, 1960).
- Erora laeta* (Edwards), Riotte, 1961, 15(2):92 (Algonquin Park, Ontario, May 20, 1960).
- Erora laeta* (Edwards), Roever (*partim*), 1962, 16(1):1, 4 (Ontario and Nova Scotia south to Virginia, ♀ Little River, Great Smoky Mts. Nat. Park, Sevier Co., Tennessee, 3,000', April 15, 1938, leg. Arthur Stupka; Andrew's Bald, 5,860', July 17, 1936, Great Smoky Mts. Nat. Park, Swain Co., North Carolina, July 17, 1936, leg. Siebert and Evans).
- Erora laeta* (Edwards), Small "1962" [1963], 16(3):195 (New Hampshire).
- Erora laeta*, Hessel, 1963, 17(1):43.
- Erora laeta* (Edwards) (= ♀ *clothilde* [Edwards]), dos Passos, 1964, p. 55, no. 375.
- Erora laeta*, Clench, 1966, p. 9 (Powdermill Nat. Res., Pennsylvania).
- Erora laeta* (Edwards), Clench, 1968, p. 4 (Powdermill Nat. Res., Pennsylvania).
- Erora laeta* (Edwards), dos Passos, 1970, p. 35.
- Erora laeta* (Edwards), F. M. Brown and P. A. Opler, 1970, p. 19-77, (Type in Acad. Nat. Sci. Philadelphia).
- Erora Scudder laeta* (Edwards), Riotte, 1970, p. 3.
- Erora laeta* in A. B. Klots, 1970, the rarest of Northern butterflies, newsletter Mich. Ent. Soc. 18(2):1-3.
- Erora laeta*, Patterson, 1971, 25(3):222; "on May 19, 1968 while I was walk-

ing along a grassy wood road about 8 mi SW of Wellsboro [Northern Pennsylvania], in an area much grown up to mixed hardwood brush, a fresh female *Erora laeta* literally dropped into the road in front of me. Later that same year on July 29, a worn male was collected and another sighted on blossoming hardhack [*Spiraea tomentosa*] in a nearby wet field."

Erora laeta (Edwards), Sullivan, 1971, Journ. Lep. Soc. 25(4):295 (Allegheny Co., NW corner of state while catching *Speyeria idalia*).

Erora laeta, Sullivan, 1971 *ibid.* 25(4):296 (Allegheny Co., North Carolina, July 1, 2,700' ♀, Ash Co., 2,700' ♂).

Erora laeta (Edwards), Lewis, 1973 (*partim*), p. 218, Lycaenidae pl. 18, figs. 14, 18 (Quebec to Arizona, Mexico and Central America).

Erora laeta Edwards, Brower, 1974, p. 20 (Streaked Mt., near Paris, 22 July (Smith); Dallas Plt. (Rangeley) 16 June, ♀; T2R12 (Greenville), 4 July, ♂; Orono, 18 May; Lincoln (Clayton); Bar Harbor, 19 May, ♂, 25 May, ♀ all Maine.

Erora laeta (Edwards), T. C. Emmel in Howe, 1975, p. 306, pl. 50, fig. 21 ♂ (range does not approach that of *quaderna*).

Erora laeta, Bowers, 1978 (abundance, Carroll County, nr. Bartlett, New Hampshire; habits).

Erora laeta (Edwards), Drees and Butler, 1978, p. 202 (Cabell, Greenbriar, Kanawha, Pendleton and Randolph Counties, West Virginia, V-5 to VII-26).

Erora laeta, Oosting, 1979, p. 160 (Ontonagon Co., Michigan, 27 May 1975 (one female; no *Fagus* present; *Corylus* present).

Erora laeta Miller, 1980, pp. 209–216 (general discussion and differentiation).

Taxonomic notes: The type of *Thecla laeta* Edwards (Figs. 21–22) is in the Carnegie Museum. It was discussed by Brown and Opler (1970). The type locality is London [Ontario]; the label on the type reads only "Canada." (At that time what is now called Ontario was known as "Upper Canada.")

The type of *Thecla clothilde* Edwards cannot be found in the Carnegie Museum. It was taken near Quebec by Rev. M. Provancher presumably in 1862 and probably at Cap Rouge where he lived. Provancher's collections of insects are in the College of Levis and the Quebec Public Museum, but Rev. J. C. E. Riotte who kindly examined these collections advises us (in litt.) that the type of *clothilde* is not in either of these collections. Consequently it must be deemed to have been lost or destroyed. We see no necessity to erect a neotype.

For many years the butterfly that we now call *E. quaderna sanfordi* dos

Passos was known, but classified as *E. laeta*. This has caused considerable confusion, and specimens of both were mixed together. We note that a record of "*laeta*" by Aaron (1884) from Atlantic City, New Jersey was the basis for various authors (Edwards 1884; French 1886; Scudder 1889; Maynard 1891; Holland 1898; Skinner 1898; Holland 1931; Comstock 1940; Field 1941) attributing *laeta* to New Jersey. We have always mistrusted this record, which is from an entirely wrong environment. A note from Harry Clench at the Carnegie Museum (in litt. 24 July 1978) reads: "We have a female *Erora* that is labelled Atlantic City, N.J., ex coll. Skinner, ex coll. A.N.S.P. The A.N.S.P. collection had much (all?) of E. Murray Aaron's collection, and I believe he was the source of "Atlantic City" as a locality for *laeta*. This specimen, however, is a *quaderna sanfordi*!" We believe that this Atlantic City record and any New Jersey records based on it (e.g. "Cape May") are erroneous.

Some additional records follow, based on specimens in various museums and private collections. We are indebted to J. Donald Lafontaine and A. C. Sheppard for most of these. BM = British Museum (Natural History). CNC = Canadian National Collection. LEM = Lyman Entomological Museum, McGill. UM = University of Montreal. ACS = Collection, A. C. Sheppard. PH = Collection, Peter Hall. RL = Collection, Ross Layberry.

New York. 1 ♂, Long Lake, Adirondack Forest Preserve, Upper New York State, May 22, 1977, leg. P. Hall (CNC). *New Brunswick.* Edmundston, leg. Henry Hensel, 1 ♂ June 12, 4 ♀♀ June 13–16 (BM). *Quebec.* St. Hilaire (1,500 ft) 24.V.88, 24.V.02, 24.V.10, 24.V.11, ex A. F. Winn Coll., (LEM). 1 ♀ Meach Lake, 12 mi NW Ottawa, Ont., 25.V.1968, leg. A. Hanes (CNC). 1 ♀ Duncan Lake, 7 mi WNW Wakefield, Masham Twp. 1.V.1977, leg. D. M. Wood (CNC). 1 ♂ Gatineau Park, 6 mi N. of Aylmer, 27.V.1978, leg. P. Hall (PH). 1 ♀, Gatineau Park, 29.V.1978, leg. R. Layberry (RL). Parc du Mont Tremblant, 27.V.1957, 1 ♀ and 2.VI.1958, 1 ♀, leg. A. Robert (UM). Vernet (Papineau Co.) 24.VII.1941, 1 ♀, on *Spiraea* blossom, leg. A. C. Sheppard (ACS). 1 ♂, 4 mi S. of Lost River (Argenteuil Co.) 12.V.1957, on Dandelion blossom, leg. A. C. Sheppard (ACS). *Maryland.* Dargan, Washington County, 14 April, 1977, Robert S. Simmons.

Field studies; localities: Field studies were made by the authors separately and together, and accompanied at times by others, beginning in 1934 and ending in 1968. These were at two localities; others were visited but with no results for *laeta*.

1. Near West Bridgewater, Windsor County, Vermont, up a woodroad toward Killington Peak (Rutland and Woodstock topographic quadrangles). The woodroad ascends generally westward and eventually runs into trails up Killington Peak. *E. laeta* was found along the woodroad between 1,600 and 1,900 ft altitude. This locality was first found by A. C. Frederick and

L. J. Sanford. It has been referred to by them and others, and specimens from there labelled, as "Bear Mt. near Bridgewater Corners" and "Mt. Killington" (Field, 1941, pp. 305, 315).

2. Near Sandgate, Bennington County, Vermont (Equinox topographic quadrangle). We refer to this as "Mt. Equinox," as have other collectors. From Sandgate a country road runs northeastward and eastward through a community called Beartown; and from this a woodroad ascends to the saddle (2,300 ft altitude) between Mt. Equinox and Mother Meyrick Mountain. *E. laeta* was found most commonly at this saddle, but also below it along woodroads on both sides down to about 1,900 ft altitude. This locality was first found by the veteran student of lycaenids, J. C. Cook; and A. C. Frederick also collected there. Their material was mostly labelled "Mt. Equinox, near Manchester, Vermont, 2000 ft." and was so referred to by Field, loc. cit.

We learned about these localities through the kindness of Messrs. Cook, Frederick and Sanford. During our fieldwork considerable plant-successional changes took place at both localities as old meadows and clearings were invaded by trees and shrubs and the woodroads became more shaded. In addition the woodroads at both localities were heavily bulldozed because of logging operations higher up. However, these changes did not appear to affect the *laeta* except, perhaps, to concentrate them in open spaces.

In all, the authors put in, separately or together, a total of 52 days at these localities. *E. laeta* was taken or merely seen on 16 occasions, as noted below.

- 1934, 22-23 May, Mt. Equinox, none
- 14 June, Mt. Equinox, none
- 1936, 29 May-1 June, Mt. Equinox, none
- 1938, 4 June, Mt. Equinox, none
- 5 June, W. Bridgewater, none
- 1947, 29 May, Mt. Equinox, none
- 1 June, W. Bridgewater, none
- 1949, 4 June, Mt. Equinox, none
- 5 June, W. Bridgewater, 1 ♂, 1 ♀, both worn
- 10 June, Mt. Equinox, 1 ♂, 2 ♀♀ (1 very fresh), 2 seen
- 1950, 9 June, Mt. Equinox, none
- 10 June, Mt. Equinox, none
- 11 June, W. Bridgewater, none
- 12 June, Mt. Equinox, none
- 1951, 19 May, Mt. Equinox, 1 ♀ (worn), 1 ♀ (very fresh), 1 ♂ seen
- 26 May, Mt. Equinox, 2 ♀♀ (very fresh), 1 seen
- 28 May, W. Bridgewater, none

- 5 June, Mt. Equinox, 5 ♂♂, 9 ♀♀, mostly very fresh
 20–21 June, Mt. Equinox, 1 ♀ (worn), 1 ♀ (very fresh)
 1952, 23–24 May, Mt. Equinox, none
 6 June, Mt. Equinox, none
 1953, 29 May, Mt. Equinox, none
 14–15 June, W. Bridgewater, 1 ♂ seen
 1955, 7–9 June, Mt. Equinox, none
 1956, 16 June, Mt. Equinox, none
 17–18 June, W. Bridgewater, 1 ♂, 1 ♂ seen
 1957, 9 June, W. Bridgewater, none
 10–11 June, Mt. Equinox, 20 ♂♂ and ♀♀, mostly fresh to very fresh,
 several more seen
 1960, 17–19 June, Mt. Equinox, none
 1961, 17–18 June, Mt. Equinox, 14, mostly ♀♀ and very fresh, 2 seen
 19 June, W. Bridgewater, 2 seen
 1963, 11 June, Mt. Equinox, 1 seen
 1966, 12 June, Mt. Equinox, 16 ♂♂ and ♀♀, some very fresh, others seen
 1967, 12–15 June, Mt. Equinox, none
 1968, 31 May, Mt. Equinox, none
 3 June, Mt. Equinox, none

Only days of favorable weather when *laeta* might have been flying are listed. All records are, of course, of the first generation. No consistent efforts could be made to find the second generation; on two visits to Mt. Equinox in mid-July none were seen. We found *laeta* in only 8/18 years, but suppose that it was present in all years. Only four years: 1951, 1957, 1961 and 1966 were "good." The record for 1951 at Equinox is notable, for the first specimen, a somewhat worn ♀, was taken on 19 May and a very fresh one on 21 June, a flight period of more than a month. During the first part of the flight period Shadbush *Amelanchier canadensis* (L.) comes into bloom, followed by the Wild Cherries *Prunus serotina* Ehrh. and *pensylvanica* L.

Associated butterflies: *E. laeta* appeared to be preceded in flight, at the same altitude levels, by *Celastrina ladon* (Cramer) and *Erynnis brizo* (Boisduval and LeConte) and *juvenalis* (Fabricius). A few individuals of *Pieris napi oleracea* Harris precede *laeta*, but occasional very heavy flights of this species may coincide with flights of *laeta*. *Pieris virginiensis* Edwards was taken only once (1951). Fresh *Poanes hobomok* (Harris) and *Amblyscirtes samoset* (Scudder) and *vialis* (Edwards) flew consistently with fresh *laeta*. Lower down on the woodroads fresh *Papilio glaucus* L. of the small northern form, *Boloria selene* (Denis and Schiffermueller) and *bellona* (Fabricius), *Melitaea harrisii* (Scudder) and *Phyciodes tharos* (Drury) were be-

ginning to fly and occasionally strayed up into *laeta* territory. Toward the latter part of the *laeta* flight season a phenotypically very mixed population of *Limenitis arthemis* (Drury) and *astyanax* (Fabricius) became common. We conclude that the flight period of *laeta* lasts about a month to five weeks beginning a week to ten days after the first flight of *C. ladon* and *E. brizo* and *juvenalis*.

Our studies and the observations of other collectors indicate that *laeta* populations show considerable fluctuation from year to year, with occasional years when there is almost an outburst with large numbers occurring. Opposed to this is the possibility that, since *laeta* is essentially a tree-living species, a year of apparent sudden abundance is merely one when a chance combination of circumstances brings (or keeps) a large number of individuals down at ground level for hardening the wings, drinking and basking. Very likely much of the seemingly abnormal abundance is due to the fortuitous presence of the collector at just the right time.

The two *laeta* localities are in what is essentially the Beech-Birch-Maple hardwood forest that covers large areas in the Canadian Life Zone (Merriam), Coniferous Forest Biome (Shelford) and Canadian Biotic Province (Dice). The localities contain, however, large admixtures of the Transition Life Zone, particularly in the warmer localities at lower elevations. This is in accordance with the known geographic distribution of *laeta*, since such an environment occurs far southward along the Appalachian and Allegheny mountains and highlands.

Associated plants: The chief trees and shrubs serve as an index to the environment. Some of these, such as Red Spruce (*Picea rubens* Sargent), Sugar Maple (*Acer saccharum* L.), Mountain Maple (*Acer spicatum* Lamarck), Striped Maple (*Acer pensylvanicum* L.) and White Birch (*Betula papyrifera* Marshall) are characteristic dominants of this lower Canadian Zone formation. Other important woody plants were willow (*Salix*) two species, Quaking Aspen (*Populus tremuloides* Michaux), Beaked Hazelnut (*Corylus cornuta* Marshall), Gray Birch (*Betula populifolia* Marshall), Cherry Birch (*Betula lenta* L.), Yellow Birch (*Betula lutea* Michaux), Beech (*Fagus grandifolia* Ehrhart), Gooseberry (*Ribes* sp.), Shadbush (*Amelanchier canadensis* L.), Raspberry (*Rubus idaeus* L.), Flowering Raspberry (*Rubus odoratus* L.), Blackberry (*Rubus allegheniensis* Porter), Wild Black Cherry (*Prunus serotina* Ehrhart), Wild Red Cherry (*Prunus pensylvanica* L.), Red Maple (*Acer rubrum* L.), Maple-leaved Viburnum (*Viburnum acerifolium* L.), Hobblebush (*Viburnum alnifolium* Marshall) and Common Elder (*Sambucus canadensis* L.).

The mixed Canadian-Transition zonal status of the region studied at Mt. Equinox is also indicated by other butterflies found there. *Cercyonis pegala* (Fabricius) occurred in grassy meadows about a half mile below the *laeta* area as a very mixed population. In a considerable series (taken later in the

season) specimens range all the way from the northern “*nephele*” type lacking an orange patch on the forewing to the more southern “*alope*” type with a large orange patch. We personally consider these two types, *alope* (Fabricius) and *nephele* (Kirby) to rank as subspecies. In any event, they here intergraded in a narrow tension zone. The same was true of the population of *Limenitis arthemis* (Drury) which occurred very commonly, chiefly below the restricted *laeta* area, as a very mixed population of *L. arthemis arthemis*, the northern, white-banded subspecies, and *L. arthemis astyanax* (Fabricius), the more southern, non-banded subspecies. In a large series collected here occurred almost every possible intergradation between these two phenotypes. In the West Bridgewater area a large series of *Melitaea harrisii* Scudder was taken over several years in a meadow below the *laeta* area. They show a great variation between lightly marked individuals like the southern population *ligetii* Avinoff and dark individuals like the northern *albomontana* Avinoff. We have some doubt about recognizing *ligetii* and *albomontana* as “good” geographic subspecies; there is too much intergradation all along the line between them.

Foodplant: For many years only the record of Mousely (1923) pointed to beech as the *laeta* foodplant. On Mt. Orford, Quebec, Mousley watched a *laeta* female deposit an egg on the underside of a beech leaf near the base and midrib. The egg was taken; the larva began feeding on beech, but soon died. We therefore paid special attention to beech, but never saw females on it. A number of captive females were confined on it both in sleeves in the field and in cages at home. Other potential woody foodplants were also tried, but with no luck. Most of the females were very fresh, and probably had never mated; one worn one had apparently already deposited her eggs. Then in 1951 a female laid (8–10 June) about 20 eggs on both beech and beaked hazel leaves and also the screen of the cage. The eggs hatched 14–19 June. A number of the larvae were lost, but several ate either beech or beaked hazel leaves through the first instar. After that those on beech ceased to feed. One of these, transferred to beaked hazel, ate that and survived; the other beech-eaters died. One larva on beaked hazel died in its second instar, three survived into the third instar, and two others survived to pupate. One of the pupae died, but the other survived to eclose as a rather small female on 4 August, under the care of Dr. Frederick Rindge. We afterward guessed that some of the beech leaves, which came from Pelham, New York, were polluted. (This we know to have been the case with some pine foliage from there used for other larvae.) The beaked hazel, brought from Vermont and Connecticut, was clean enough. It was noted that three of the larvae, including the one that developed into an adult, fed partly on developing hazel fruits, which is consistent with Whittaker’s record of finding a *laeta* larva on a beech fruit (see below). During later fieldwork in 1951 and subsequent years a great deal of time was spent in examining both beech

and hazel minutely, but no eggs or larvae were found on either. There was abundant beaked hazel, as well as beech, in the *laeta* areas.

In 1972 or 1973 Dr. R. H. Whittaker found a larva on beech in the Hubbard Brook Experimental Forest in the vicinity of West Thornton, 22 km north of Plymouth, Grafton County, New Hampshire. This was in the course of a Hubbard Brook ecosystem study, forest part (Whittaker, R. H. et al. 1974, Ecological Monographs, 44:233–254). Dr. Whittaker kindly sent us the following information: "We were felling trees, including beech, for detailed dimensional analysis; a part of this was the separation of sample branches into wood, twigs with leaves, and fruit. I was plucking and bagging fruits, and had tossed a fruit with larva into the bag when my mind connected two points; it was a lycaenid larva, and the larva was associated with beech and *Erora*. The larva, retrieved, was found to have been feeding on the soft papillae of the beech fruit. It continued to feed on these for a few days." The larva then died and was preserved and deposited in the Peabody Museum of Yale University. Sent to us through the kindness of Sidney Hessel, it was compared with our preserved *laeta* larvae and photographs and positively identified as *laeta*.

We sent a questionnaire to a number of collectors who had taken *laeta*. Many of these answered that there had been beech in the environment; none stated that there was no beech; fewer had noticed beaked hazel. Edward Voss kindly showed us the locality in Bliss Township, Emmet Co., Michigan where he and Wagner had collected *laeta* (Voss and Wagner 1956). Beech was present, but beaked hazel was not. The fact that our larvae were reared through on beaked hazel does not indicate that this is a normal foodplant—only that it is an acceptable substitute in vitro. Unfortunately our mention of *laeta* having been reared on beaked hazel has crept into print (via the grapevine) in Forbes, 1960, pp. 131–132. However, Oosting (1979) has recently recorded the presence of *laeta* at a locality in Ontonagon Co., Michigan where there is abundant beaked hazel but apparently no beech. So, the matter stands open; we consider beech to be the normal foodplant over at least most of the range, with beaked hazel perhaps a natural foodplant in some localities and circumstances.

Newly hatched larvae probably do a certain amount of leaf skeletonizing at first but are likely to switch to flowers and developing fruits. If they do not find any of these they may continue on leaves. As the rearings took place the following durations were noted: egg, 6–6.5 days; 1st instar, 4–5 days; 2nd instar, 4–5 days; 3rd instar, 4–4.5 days; 4th instar, 5.5 days, 5th instar, 11.5 days; pupa, 13 days.

Egg (Figs. 9–11): Pale, slightly greenish yellow, considerably flattened; height 0.30–0.34 mm, diameter 0.69–0.75 mm, with a somewhat variable, shallow depression surrounding micropyle. Micropyle of 5–6 unequal polygonal cells surrounded by many smaller ones. Surface of egg thickly stud-

ded with small, conical projections irregularly placed, basally connected by very fine, raised ridges. There are about 25 of these projections along an irregular line from base to termen; those around the base are slightly longer. Duration of egg stage (5 eggs) averaging slightly more than 6 days. Cf. Scudder 1889, Vol. III, pl. 65, fig. 8.

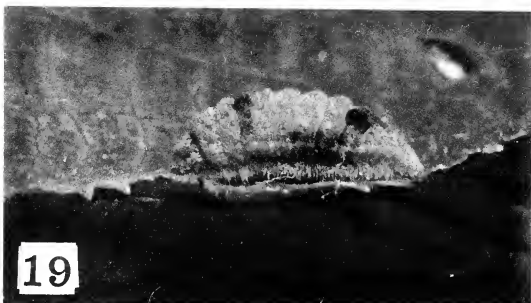
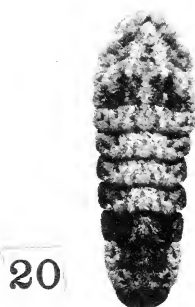
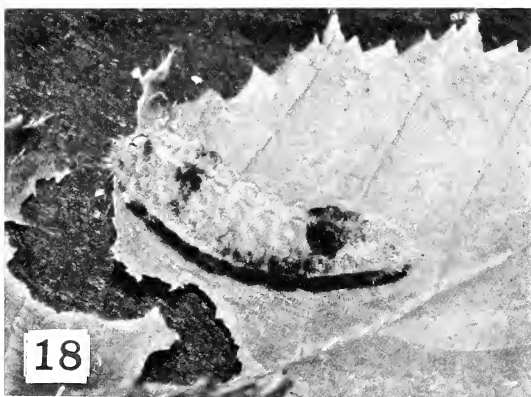
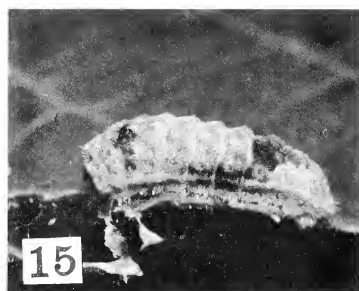
Larva, first instar (Fig. 1): Length 1.9–2.2 mm (5 larvae). Pale, greenish yellow, elongate, subcylindrical, not flattened. Head small, its connection with prothorax very lightly sclerotized. A finely reticulate area on dorsum of prothorax marking the site of the calvarium (see below) in later instars. All body segments with very long, finely spiculate setae as shown. Heavily sclerotized black lenticles as shown on prothorax, mesothorax and abdominal segments 1–7 (two each) and 8 (one). Prolegs with 4 crotchets on each side. From a preserved specimen. Average duration of instar (4 larvae) 4.5 days.

Larva, second instar (Figs. 2, 12–13): Length 2.8–4.1 mm. Pale greenish yellow with an indistinct, darker, middorsal line. Head small, almost colorless; a round dark spot at each cluster of stemmata; mandibles and bases of antennae brown. Head greatly retracted beneath prothorax. Body covered with very small, coronate chalazae, each consisting of a small, basal swelling bearing a corona of 5–9 radiating spines or teeth and a central, longer spine usually minutely spiculate and more or less curved. These chalazae are essentially colorless and almost hide the underlying skin. The slightly darker appearance of the dorsal and lateral lines is caused by the darkness of the large chalazal spines. A series of paired, slightly protuberant dorsolateral swellings on mesothorax, metathorax and abdominal segments 1–7, which bear noticeably longer central spines. Dorsal surface between these swellings slightly concave, and lateral surfaces between dorsolateral swellings and ventrolateral ridges almost flat or slightly concave. Average duration of instar (5 larvae) 4.5 days.

Larva, third instar (Fig. 14): Length 4.8–5.9 mm. Very much as in second instar, essentially colorless, the very dense coronate chalazae masking the skin color. Central spines of chalazae along dorsolateral swellings and ventrolateral ridges especially long. Average duration of instar (5 larvae) 4.2 days.

Larva, fourth instar: (Pressure of other work prevented the recording of a detailed description.) In this instar the larvae had developed a definite pattern of dark spots and except in size resembled the fifth instar larva described below.

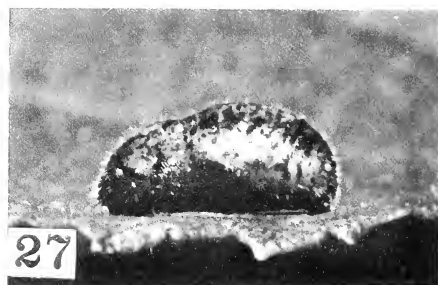
Larva, fifth instar (Figs. 3–8, 15–19): Length when mature 11.5–12.3 mm. Vesture of prothorax very short and sparse in central calvarium. This is diamond-shaped, its cephalic angle very attenuate and sharp, with concave sides, its caudal angle shorter and truncate. Skin yellowish green showing more or less through vesture depending on degree of distention of larva.



Figs. 15–20. *Errora laeta*. 15–18. Mature larvae, lateral and laterodorsal views, showing normal variation. 19. Mature larva, lateral view, a lightly marked specimen. 20. Prepupal larva, dorsal view; the prothoracic calvarium shows plainly.



Figs. 21-26. 21-22. *Erora laeta* (Edwards), type ♂, upper and under sides. 23-24. *Erora laeta sanfordi* dos Passos, holotype ♂, upper and under sides. 25-26. *Erora laeta sanfordi* dos Passos, allotype ♀, upper and under sides.



Figs. 27–34. 27–28. *Erora laeta*, pupa, dorsal and lateral views. 29–30. *Erora quaderna sanfordi*, mature larva, lateral views; Chiracahua Mts., Arizona. 31–32. *E. q. sanfordi*, pupa, dorsal and lateral views. 33–34. *E. laeta* ♀♀ displaying, from life, Sandgate, Vermont.

Vesture of coronate chalazae with their central spines particularly long along ventrolateral ridges, especially on thoracic and last abdominal segments. Dorsolateral ridges each consisting of a swelling of each segment from mesothorax posterad; these give the larva a subserrate outline. The most anterior of these swellings, on the mesothorax, is especially prominent. Similar lateroventral ridges, weak on mesothorax, extending caudad to around end of abdomen. Legs and prolegs largely hidden below these. Honey gland not present.

Dark markings quite consistent in pattern but varying in color and extent. In one larva they were bright reddish; in another darker brownish red. On or about each mesothoracic swelling a small dark area. On first abdominal segment a pair of dorsolateral patches more or less running down on each side. On each side of fourth and fifth abdominal segments a patch slightly above ventrolateral ridge with traces of dark running cephalad on third, and caudad on sixth abdominal segments. On or slightly below each ventrolateral ridge a narrow dark shade on abdominal segments 1–6, diffusing out on 7. On sixth abdominal segment a pair of wide dark patches almost confluent together dorsally, extending down on each side to about the level of the spiracles, and slightly confluent with the ventrolateral patch on sixth segment, tapering caudad on seventh and eighth abdominal segments. There was some variation in the size and extent of these patches, but they were present in all of the five mature larvae studied.

Prepupal larva (Fig. 20): The general color became darker and dingier, with the dark markings less contrasty. The larva became shorter and assumed a more broad-oval shape, more rounded laterally and dorsally. The calvarium was very noticeable. No silk girdle was spun. Duration (2 larvae) 2 days.

Pupa (Figs. 27–28): Short, blunt and rounded, characteristically lycaenid. Integument more or less covered with fine, raised reticulations which, being more heavily sclerotized than the rest of the cuticula, account for the darker appearing areas. Setae arising almost entirely from chalazae at the intersections of reticulations. Setae rather sparse, there being, for example, about nine along the middorsum of the third abdominal segment, which measures 0.91 mm; setal lengths 0.10–0.21 mm. All setae simple, very finely spiculate, gradually tapering to fine tips. None of the specialized and complex sensillae present in some lycaenoid pupae (cf. Downey and Allyn 1973, many figs.) were noted. (The pupa of *E. quaderna sanfordi* had a number of “sensillae companiformia” (ibid., Fig. 62) chiefly in small clusters about the abdominal spiracles). We were also unable to find any of the small, paired pores noted by Downey and Allyn dorso-mesad of the abdominal spiracles. The stridulating structures were not studied in detail because of our reluctance to dissect the specimens. They have the caudal margin of the 5th abdominal

segment raised and more strongly sclerotized than the remainder of the segment. Entad from this is the grating surface, which is heavily sclerotized and bears many fine, uniform, parallel ridges running entad (cf. Downey and Allyn, op. cit., Fig. 24). This extends down on each side to slightly below the level of the spiracle. The file opposed to these ridges was not studied. No trace of a honey gland was found on the dorsum of segment seven. Cremasteral hooks are of the conventional form, each with a flattened, rounded tip bent strongly basad, on a low, rounded protuberance on each side of the anal slit. Each of the two pupae was formed on a leaf, but no silk girdle was seen.

Adult behavior (Figs. 33–34): A majority of other collectors' records, as well as our own, mention specimens of *laeta* as having alighted on bare ground and being seen only when they flew up, often to the collectors' surprise because their cryptic coloration made them inconspicuous. In 18/19 of our records of this the specimen was on dry earth or gravel, only one being on damp earth. Quite a number of other collectors, however, mention damp earth or mud. The late J. H. Cook described to us (in litt.) a number of *laeta* in the Mt. Equinox area flying up from a damp place where he believed there was horse urine. We tried several times to attract *laeta* in areas where they were flying by wetting the ground with water or urine, but with no success, although we did attract numbers of *Celastrina ladon*. Perhaps we should have had a horse. The majority of the specimens seen on the ground were females, and the majority of these were teneral, i.e. very recently emerged from the pupa, and emitting meconium when kept alive. They were also very tame, crawling about slowly, so that we were able to crawl up, watch them very closely and photograph them from only a few inches away. Some were making probing motions with the proboscis (perhaps only adjusting it) but others were not. We have no doubt that individuals on wet earth or mud may drink, but we did not see this. Those on dry ground seemed to be basking, sometimes orienting themselves across the line of the sun, sometimes opening the wings so as to receive a maximum of sun on the upper surface. Such an action by a female may also serve for visual attraction of a male (Figs. 33–34). The large proportion of teneral females to males probably resulted from the males having emerged earlier from the pupae and having flown to rest on foliage higher up where they were not seen.

An extraordinary experience of Bowers (1978) is highly pertinent. Mr. Bowers and Reginald Webster, collecting near Bartlett, Carroll County, New Hampshire on 21 May 1977, along abandoned dirt roads through beech woods, saw over 80 *laeta* of which all but two were females, some quite worn, while others looked freshly emerged. The females were resting on the ground, chiefly on mud, where they were presumably drinking, and are described as very easy to catch, some not even flying up when the net was

clapped over them. The day was sunny, hot (33°C) and humid, so that the *laeta* were presumably thirsty. The only two males seen flew much more actively than the females, only occasionally alighting on vegetation.

Of 27 of our specimens only 8 were caught as they rested upon or flew from the leaves of various plants. In 4/8 of these cases the leaves were of such low species as Wood Nettle (*Laportea canadensis* L.), Canada violet (*Viola canadensis* L.) and Raspberry (*Rubus idaeus* L.). In the other four cases the individuals were resting on the leaves of Mountain and Sugar Maples (*Acer spicatum* and *saccharum*) five to eight feet above the ground. One of these specimens, on a maple leaf, was caught entirely unexpectedly (in the true *laeta* tradition) when a collector made a sweep at a high-flying geometrid and found not only the moth but a scale-perfect *laeta* in his net—his first! Perhaps the individuals resting on high leaves were basking where there was more direct sunlight—a phenomenon we have noticed in some *Callophrys* (*Incisalia*) *henrici* (Grote and Robinson), which are much given to basking on the shiny leaves of Holly and Laurel.

This persistent habit of *laeta*, especially when teneral, of resting on the ground may largely explain the irregular and unexpected records of large numbers. Perhaps the adults are on the ground for only a short time when the right combination of heat, sun and thirst keeps them there. Most of the time large numbers may be present, but unseen, high in the trees. We think that the species is more a dweller in the forest canopy than has been realized.

Only once was anything like a courtship observed; a male and a female were fluttering about each other in a small, sunny spot along a shaded woodroad. After about two minutes they flew up high together and disappeared among beech foliage overhead. Perhaps most courtships and matings take place high up.

We were long puzzled by an apparent absence of flower-visiting. Captive individuals fed well on honey and sugar water. Numerous flowers such as those of Shadbush, Wild Cherries, Violet, Blackberry, Raspberry and Wintercress (*Barbarea vulgaris* Brown) were available in abundance but were not visited. Finally, on 12 June, 1966 a large number of *laeta* were seen visiting the flowers of a Wild Cherry several feet above the ground; 16 specimens were taken by W. D. Field and the junior author. Ferguson (1954, p. 197) records *laeta* in Nova Scotia visiting Blackberry flowers; Sullivan (1971) saw it on Hardhack (*Spiraea*) flowers in Pennsylvania; Covell (in litt.) records it visiting Oxeye Daisy and Wild Hydrangea in Kentucky; and Sheppard on *Spiraea* and Dandelion in Quebec. For comparison be it noted that *E. q. sanfordi* is an eager flower visitor, especially on *Amelanchier* and *Ceanothus*.

Fluctuation in numbers: Our own records, as well as those of other collectors, seem to indicate considerable variation in numbers from year to

year. Most records are of only one or two individuals; but occasionally and unexpectedly the species will be found very common or abundant. It is always possible, as noted above, that individuals are present, but unobserved, being high in the beech foliage, courting or ovipositing. We suspect that when collectors watch among high foliage they will see many more *laeta* than otherwise.

Voltinism: Our own data on voltinism are meagre. Our one reared *laeta* emerged in August. Two visits to the Mt. Equinox locality in mid-July revealed no *laeta*. Enough records are available, however, to indicate that *laeta* is bivoltine, with a second generation in July–August. Dr. Charles Covell tells us (in litt.) of over a hundred *laeta* taken on and near Big Black Mountain, alt. 4,145 ft, Harlan County, Kentucky in early to middle July, obviously second generation; only two Spring specimens have been taken, 24 April, 1976.

Distribution, summary: As discussed above, *laeta* is essentially a species of the beech-birch-maple forest that characterizes lower Canadian Zone, and of the very extensive ecotonal regions where this mixes with upper Transition Zone. In Canada it is found in Nova Scotia, New Brunswick, Quebec and Ontario, not extending northward into the Canadian Zone regions of dominant coniferous forest. In northern Michigan it flies where there are strong Canadian Zone elements, and "Great Lakes Forest." In New England it occurs in Maine, New Hampshire, Vermont and western Massachusetts, following Canadian Zone through the Green Mts. and Berkshires. It is not recorded from Connecticut or Rhode Island. We suspect, however, that it may occur in extreme western Connecticut and perhaps eastern New York where the high ridge of the Taconics runs southward from the Berkshires, carrying considerable Canadian Zone and beech, at altitudes up to 2,316 ft. Its occurrence in the Catskill Mts. is quite as expected; it must occur widely in the Adirondacks. The outlying records from the Finger Lakes region (Ithaca, Cortland, Wickwire) are in a region where some Canadian Zone elements occur on high hills, but do show that *laeta* has been able to maintain colonies that are offshoots of the main lower Canadian Zone pattern. It has not been reliably recorded from New Jersey (we regard the Aaron record from Atlantic City and Cape May as false) but it may well occur along the Kittatinny Ridge in the north. It occurs in the highlands of Pennsylvania. The single record from Maryland (Dargan, Washington County, 14 April 1977, leg. Robert S. Simmons, in litt.) is in semi-highland environment with beech present. Thence *laeta* expectedly follows the Appalachian and Allegheny highlands southward through West Virginia, Kentucky, Tennessee and North Carolina to Georgia. It may occur in the Cumberland Plateau in Tennessee and the Ozark Plateau in Missouri and Arkansas.

Erora quaderna quaderna (Hewitson)

Thecla quaderna Hewitson, 1868, p. 35.

Thecla attalion Godman and Salvin, 1887, 2:60; 3:pl.35, Figs. 19–20.

The present paper deals with *E. quaderna* only because of its relationship with *E. sanfordi* dos Passos, which we place as a subspecies of *quaderna*. The nominate subspecies occurs in central Mexico and southward. Speculations as to its phylogeny have been covered above under the genus *Erora*. Some data about *E. q. quaderna* have turned up, however, in the course of our studies and these are presented below.

Type material: The types (both unique) of *Thecla quaderna* and *T. attalion* were studied at the British Museum (Natural History) where T. G. Howarth very kindly picked them out and dissected them for us. That of *quaderna*, a female, is dissection T.G.H. 656 (1964); that of *attalion*, a male, is dissection T.G.H. 657 (1964). We compared these with specimens of *quaderna* from the United States National Museum very kindly dissected and sent on loan by W. D. Field. These were: a male, dissection W.D.T. 475 from Guatemala; and three females, dissections W.D.F. 476, 477 and 478 from Mexico and Guatemala. In coloration and pattern the specimens agreed well with the types of the corresponding sexes (making some allowance for discoloration and wear) and similarly with each other. In the genitalia we found only minor differences which seem well within the limits of individual variation. The male differed from the *attalion* type only slightly in the amount of angulation of the ventrocaudal angle of the valva. The females differed from the *quaderna* type only in minor details of the fine toothing and terminal spines of the signa. We consider these specimens and the types of *quaderna* and *attalion* to be conspecific, and *attalion* to be a junior synonym of *quaderna*.

Clench (1943, p. 223) "selected" the type locality of *quaderna* as Tancitaro, Michoacan, Mexico. We accept that designation because that locality is within the known range of the species and is one from which specimens identified with the species have been taken (Code, 72E). In addition that locality is about 365 miles from Orizaba, the type locality of *attalion* which we consider the female of *quaderna*.

We note, incidentally, that the types of *Thecla aura* Godman and Salvin (1887) a female from Irazu, Costa Rica and of *Erora gillottae* Riley (1924) a male, from Mt. Irazu, Costa Rica, were also compared with our material and with the types of *quaderna* and *attalion*, since it was believed that they might be related. They are certainly not conspecific with *quaderna* or *caudata*, and show such genitalic differences that we believe that they do not belong in *Erora*.

Environmental data: Mr. Harry K. Clench very kindly made available to

us some of his unpublished notes and observations of *E. quaderna quaderna*. These were made 5 air miles north of Zimapan, Hidalgo, Mexico, about 2,140 m altitude, 12 and 21 January 1966 by him and Lee D. Miller. In all, 16 *quaderna* were taken. The area is in a small, northward-facing valley clothed with oak-pine-juniper "chaparral" (low, open, scrubby forest). The *quaderna* were almost exclusively above 2,140 m alt. They were noted as being associated with one or more species of the small-leaved *Quercus*; and Clench (correctly, it now appears) believed that this was the most likely foodplant. These data agree well with our own from Arizona and with remarks by others. It seems reasonable to assume that this very widespread live oak-pine-juniper habitat is the home of *quaderna* wherever it occurs. This contrasts with the "cloud forest" habitat cited by Miller for *caudata*.

Erora quaderna sanfordi dos Passos, 1940

Figures 23–26, 29–32

Thecla laeta Edwards (*partim*), 1883, 3(1):8 (Ft. Grant, Cochise Co., Graham Mt., Arizona, leg. H. K. Morrison).

Thecla laeta Edwards (*partim*), 1884, p.[336] (Mt. Graham, Arizona, leg. Morrison).

Thecla laeta Edwards (= ♀ *clothilde* Edwards), Edwards (*partim*), 1884, p. 299, no. 374 (Arizona).

Thecla laeta Edwards, French (*partim*), 1886, p. 277, no. 114 (Arizona).

Erora laeta, Scudder (*partim*), 1889, 2:821, pl. 23, fig. 2 (Mt. Graham, Arizona).

Thecla laeta Edwards, Skinner (= ♀ *clothilde* Edwards) (*partim*) 1898, p. 50, no. 306 (Arizona).

Thecla laeta Edwards, Holland (*partim*), 1898, p. 249, no. (36), pl. 29, figs. 23 ♂, 24 ♂ (Mt. Graham, Arizona).

Erora laeta (Edwards), Elrod (*partim*), 1906, p. 131 (Montana and Colorado, *fide* Dyar; Arizona).

T[hecla] laeta Edwards, Coolidge (*partim*), 1910, 42(11):374 (Huachuca Mts., Cochise Co., July; Montezuma Canyon, Mt. Graham, Graham Co.; Chiricahua Mts., Arizona).

T[hecla] (Erora Scudder) laeta Edwards (*partim*) (= ♀ *clothilde* Edwards), Draudt in Seitz, "1924" [1907–1924] (1920), 5:783, pl. 155i, 1044 (1924) (Arizona).

Thecla (Erora Scudder) laeta Edwards, Holland (*partim*), 1931 p. 239, no. (55), pl. 29, figs. 23 ♂, 24 ♂ (Mt. Graham, Arizona).

Erora laeta (Edwards), Comstock (*partim*), 1940, 48(1):83 (Arizona).

Erora laeta sanfordi dos Passos, 1940, p. I (White Mts. 8,000', June 21, 1936; Santa Catalina Mts. 8,500'; Chiricahua Mts., April 7; Chiricahua,

- Arizona, July 7, 1933, leg. *ex* Sternitzky; southern Arizona, leg. Poling, *ex* J. Dahl; Mud Springs, Santa Catalina Mts., Arizona, 6,500', July 17–20, 1916; Silver City, New Mexico, leg. R. T. Kellogg).
- Erora quaderna*, Field (*partim*), 1941, 34(2):303, pl. 1, figs. 4, 5, 6, 8; pl. 2, figs. 5–8; pl. 3, figs. 11–13 (Mt. Graham, Chiricahua Mts., Prescott, Oak Creek Canyon, Santa Rita Mts., Paradise, Redington, Palmerlee, Senator, Santa Catalina Mts., Huachuca Mts., Arizona; New Mexico; Utah).
- Erora quaderna sanfordi* dos Passos, Clench, 1943, p. 223.
- Erora quaderna*, Bauer, 1954, 26(3):95–102, pl. 101 (Mingus Mt., Arizona).
- Erora Scudder laeta* Edwards *quaderna* Hewitson, Martin and Truxal, 1955, p. 23 (Arizona, March–July; California, March).
- T[hecla] laeta* Edwards, Forbes (*partim*), 1960, p. 131 (Arizona).
- Erora quaderna* Hewitson, Clench, 1961, p. 218, fig. 420 (*partim*).
- Erora laeta sanfordi* dos Passos, Roever (*partim*), 1962, 16(1):4 (Apache Co., Trout Creek Road, 7,500', July 4, 1958, 3 ♂♂, July 4, 1959 4♂♂, June 25 and 26, 1960 4♂♂, 1 ♀, July 22, 1961, 1 ♂, 3 ♀♀; Cochise Co., E. Turkey Creek Canyon, 6,400', April 10, 1959 2♂♂, 10♀♀, April 15, 1960 12♀♀; Pinery Canyon, Chiricahua Mts., April 15, 1960, 2♂♂, 4♀♀, Chiricahua Mts., April 15, 1960 4♀♀, June 19, 1960, 2♂♂; Coconino Co., Oak Creek Canyon, March 28, 1959 1♂, July 16, 1961 1♀; Gila Co., Peterson Ranch, 7,000', July 2, 1960 2♀♀; Graham Co., Wet Canyon, 6,000', April 23, 1961 2♀♀; Greenlee Co., Rte. 666, July 5, 1959 6♂♂, Gray's Peak Road Camp, July 5, 1959 5♂♂; 1♀ Pima Co., Madera Canyon, Santa Rita Mts. 4,400–4,600', March 8, 1959 1♂, March 19, 1960 3♂♂, Summerhaven, 7,800', Santa Catalina Mts., May 24, 1959 1♂, July 9, 1961 1♀; Pinal Co., Peppersauce Wash, 5,000', Santa Catalina Mts., April 18, 1961 1♀; Santa Cruz Co., Madera Canyon, Santa Rita Mts., 5,600–6,400', March 29, 1959 3♂♂, April 9, 1959 4♂♂, 28♀♀, April 10, 1959 1♂, 32♀♀, April 3, 1960 8♀♀, April 9, 1960 3♀♀, July 6, 1960 2♂♂, 7♀♀, July 9, 1960 4♀♀, July 31, 1960 2♀♀, April 6, 1961 12♀♀, Arizona).
- Erora quaderna*, Field, 1962 (Arizona).
- Erora quaderna*, (Hewitson), Hubbard 1965, Journ. Lep. Soc. 19(4), 232 (Pintos Altos Mts., New Mexico).
- Erora quaderna sanfordi* dos Passos, dos Passos, 1970, p. 35.
- Erora quaderna sanfordi* dos Passos, Emmel *in* Howe, 1975, p. 307, pl. 50, fig. 22 ♀ (Madera Canyon, Santa Cruz Co., Arizona A.M.N.H.).
- Erora quaderna* (Hewitson), Emmel and Emmel, 1973, p. 94 (doubtfully in California).
- Erora quaderna 'sanfordi* dos Passos, Ferris, 1976, Journ. Lep. Soc. 30(1):38–49 (Grand Co., N. Mexico, February–May). Sierra Co., July 1976. (The specimens were absolutely fresh so that it appears this species is bi-voltine. Normally collected from February to May.)

Erora quaderna sanfordi dos Passos, Miller, 1980, p. 214 (characteristics; New Mexico, Arizona, southern Utah, Mexico: Madera, Chihuahua; Loberas Summit, Sinaloa).

The citations before 1940 given above consist of references to what we now classify as *Erora quaderna sanfordi* dos Passos, known only from Utah (?), New Mexico, Arizona, northern Mexico and California (?). We regard the nominate subspecies, *E. q. quaderna*, as occurring from central Mexico southward, as noted above (under that name) and in the discussion of *Erora* phylogeny. It was known to Edwards and others of the older authors, but regarded as being merely *laeta*, so that some of their references to "*laeta*" are partly attributable to *sanfordi* when its western localities are given. It was named by dos Passos in 1940 in the combination *Erora laeta sanfordi* but since then has been variously placed as *laeta*, *quaderna* and *quaderna sanfordi*, the last combination by Clench (1943, p. 223) being in our judgment correct.

Taxonomic notes: Although Field (1941) placed *sanfordi* as a junior synonym of *quaderna* we believe it sufficiently distinct to deserve subspecific rank. For much of the following we are indebted to Harry Clench, since our own material of *q. quaderna* is scanty. On the forewings of *sanfordi* females the blue is more restricted, with only a sprinkling in the discal cell and only traces in the base of cell Cu_1 ; and in cell Cu_2 the blue extends distad to only a bit beyond the middle of the inner margin. On the forewings of nominate *quaderna* females the blue largely fills the discal cell; almost entirely fills cell Cu_1 ; and extends distad in cell Cu_2 to above about $\frac{2}{3}$ out on the inner margin. On the hindwings of *sanfordi* females, however, the blue is more extensive than in nominate *quaderna* females, especially in cell M_3 where it nearly reaches the outer margin; and the veins through this blue are more extensively lined with black. The blue of *sanfordi* is more purplish. Males of *sanfordi* have the red spots of the hindwings beneath a little smaller and duller than those of nominate *quaderna*. We have been unable to note any consistent difference in the hue of the wings beneath—not that there may not be a difference, but this green, a pigment color, seems to be rather unstable in *Erora*, fading during only a few days in flight. The same seems to be true of the color of the fringes; apart from wear these seem to fade easily from a definite red to a pale orange-red.

Field studies: Field studies of *E. quaderna sanfordi* were made 17 April–10 May, 1969, in the Chiricahua Mts. near Portal, Cochise County, Arizona, while working at the Southwestern Research Station of the American Museum of Natural History. Adults were found to be common at many places from 5,400 to 7,000 ft altitude, always in the open evergreen oak-juniper-pine scrub that covers very large areas in the lower parts of this and other Arizona mountain ranges. This represents Upper Sonoran Life Zone. The

adults were always associated with *Quercus arizonica* Sargent and *Q. Emoryi* Torrey, the dominant oaks of this habitat.

The adults were eager flower visitors, especially at *Berberis wilcoxi* Kearny, *Ceanothus integerrimus* Hook. and Arn. and *Amelanchier* in company with *Celastrina ladon cinerea* (Edwards), *Callophrys (Incisalia) augustinus annetteae* (dos Passos), *Callophrys (Mitoura) spinetorum* (Hewitson) and *siva* (Edwards) and *Erynnis juvenalis clitus* (Edwards). *Zestusa dorus* (Edwards) was also a common associate, but did not visit flowers. Its larvae were found on the same tree of *Q. Emoryi* on which a larva of *sanfordi* was found, and were reared through (Klots 1971).

When not visiting flowers the *sanfordi* adults spent much time flying about and alighting on the leaves of both the species of *Quercus*; only one individual was seen to alight on the ground, and that for only a few seconds. Even when wet soil was available the adults did not alight on it, as adults of *C. ladon* and *Z. dorus* often did. There may have been some basking on *Quercus* leaves. After a great deal of work examining *Quercus*, with the kind help of Kilian Roever (during which several *Z. dorus* larvae were found) a presumably *sanfordi* larva was found, 29 April, on *Q. Emoryi*. This was successfully reared (partly while driving to New York), pupated on 1 June and emerged as an adult *sanfordi* on 11 June. The specimen with its larval and pupal exuvia is in the American Museum of Natural History.

Mature larva (Figs. 29–30): Length with head extended forward 15 mm. Skin pale translucent green, more dilute green dorsally, showing where not covered by vesture. Head yellowish brown, darker anteriorly, paler posteriorly, darker toward mouthparts, usually almost entirely retracted beneath prothorax. Prothorax rounded, with the middorsal calvarium more or less scutelliform and somewhat depressed. Legs and prolegs pale green, yellowish toward tips. General shape onisciform, rather flattened by the lateral production of the ventrolateral ridges. Sides above these ridges slightly concave up to a pair of dorsolateral ridges along mesothorax, metathorax and abdominal segments inclusive. On mesothorax a pair of rounded protuberances at the cephalic edge, i.e. at the cephalic ends of the dorsolateral ridges; these look yellowish brown because of the concentration on them of the vesture units. Middorsal surface slightly concave between the dorsolateral ridges. Behind abdominal segment 6 the dorsolateral ridges diverge strongly to the lateral margins of the 8th abdominal segment, followed by the quite flat last segment. The ridges are most prominent at the caudal edge of each abdominal segment, giving a subserrate lateral profile. On metathorax also a pair of slightly protruding humps between the dorsolateral protrusions and the lateral margins. No dark markings; color light brown because of thick covering of brown vesture.

Most units of the vesture are, as in *E. laeta*, short coronate chalazae, i.e. each is a short chalaza with a subterminal ring of short, radiating, triangular

teeth and usually a slightly curved, stout, minutely spiculate spine terminally. Many of the pale brown vesture units have the terminal spine very short or absent. The longest terminal spines are along the ventrolateral and dorsolateral ridges. Scattered among the pale brown vesture units are a smaller number of smaller, darker, red-brown ones, not so protruding, looking like tiny red dots. No honey gland or associated structures seen. A slight silk pad was spun on a leaf, but no silk girdle was seen.

Pupa (Figs. 31–32): Exceedingly like *laeta* pupa, differing only in minor respects. Slightly more setose. Pattern of darker and lighter areas similar to, but in general slightly darker than those in *laeta* due to greater sclerotization of the raised areas and integument. A number of sensilla companioniformia (Downey and Alleyn 1973, fig. 62) were noted in small clusters about the abdominal spiracles; these were not seen in *laeta*. Stridulatory apparatus like that of *laeta*.

Volitinism: *E. q. sanfordi* is clearly bivoltine, with an early Spring generation (March, April, May) followed by a Summer one (June, July) as is shown by the records cited by dos Passos (1940), Roever (1962) and Ferris (1976).

Distribution: *E. q. sanfordi* occurs in many localities in Arizona and New Mexico. Dyar (1903, p. 40) listed it from Montana and Colorado (as *E. laeta*) and gave no other localities, East or West! Elrod (1906) merely repeated Dyar. The species cannot be credited to Montana and Colorado on this basis. Field (1941) cites a Barnes Collection specimen from Utah, leg. Bruce. This is not necessarily authentic. Similarly, a specimen in the Los Angeles County Museum from Providence Mts., San Bernardino County, California, III-22-40, leg. T. B. Blevins, is regarded by Emmel and Emmel (1973, p. 94) as mislabelled. Possibly this is the same specimen cited by Martin and Truxal (1955, p. 23) as "California, March." In any event the presence of the species in California needs verification. It is highly desirable that its extent in northern Mexico, and its southern limits there, should be investigated. Likewise, the northern extent of *E. q. quaderna*, and any possible contact between it and *E. q. sanfordi* should be investigated. Miller (1980, p. 214) gives the two localities in northern Mexico.

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American Museum of Natural History, 79th Street & Central Park West,
New York, New York 10024.

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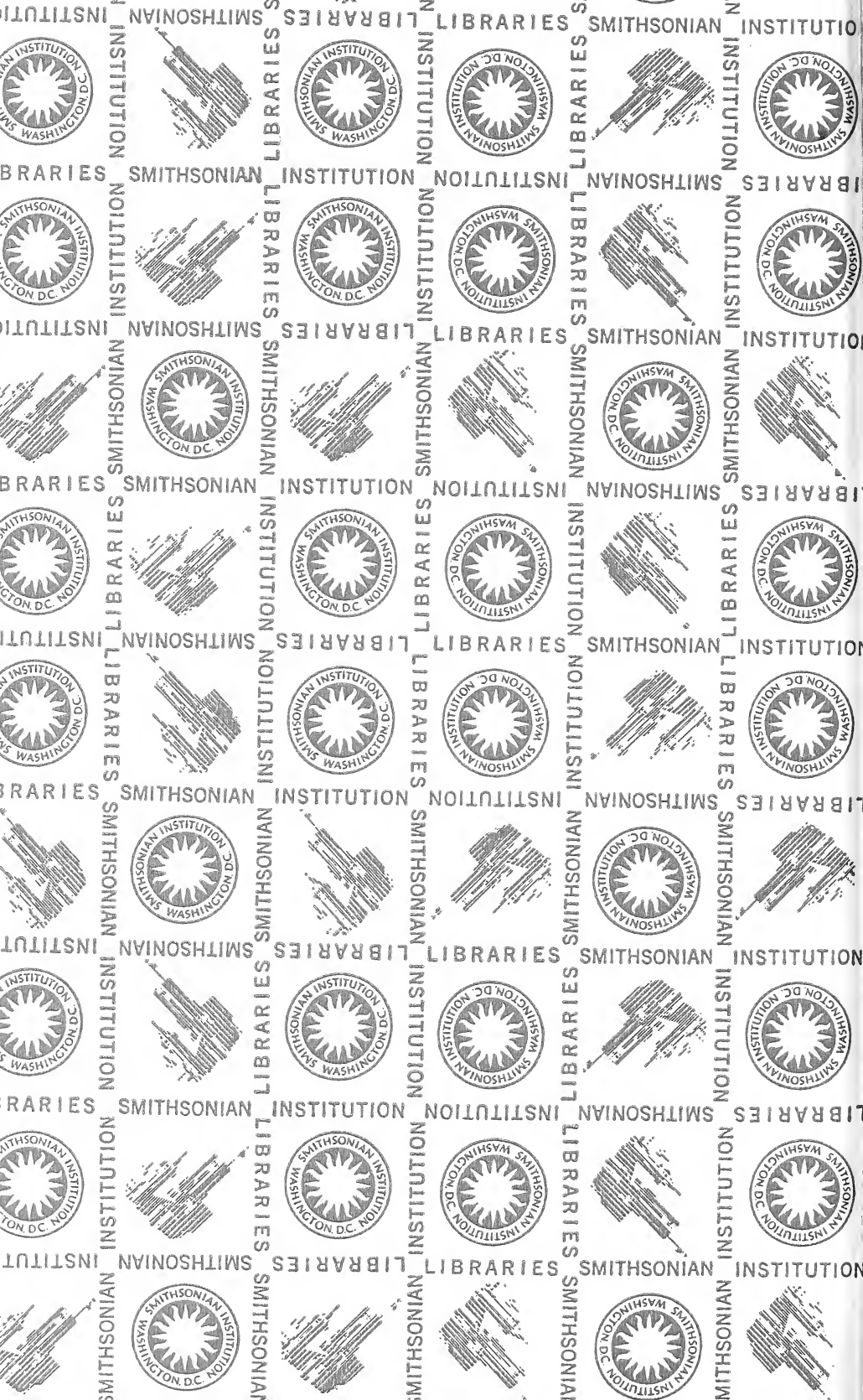
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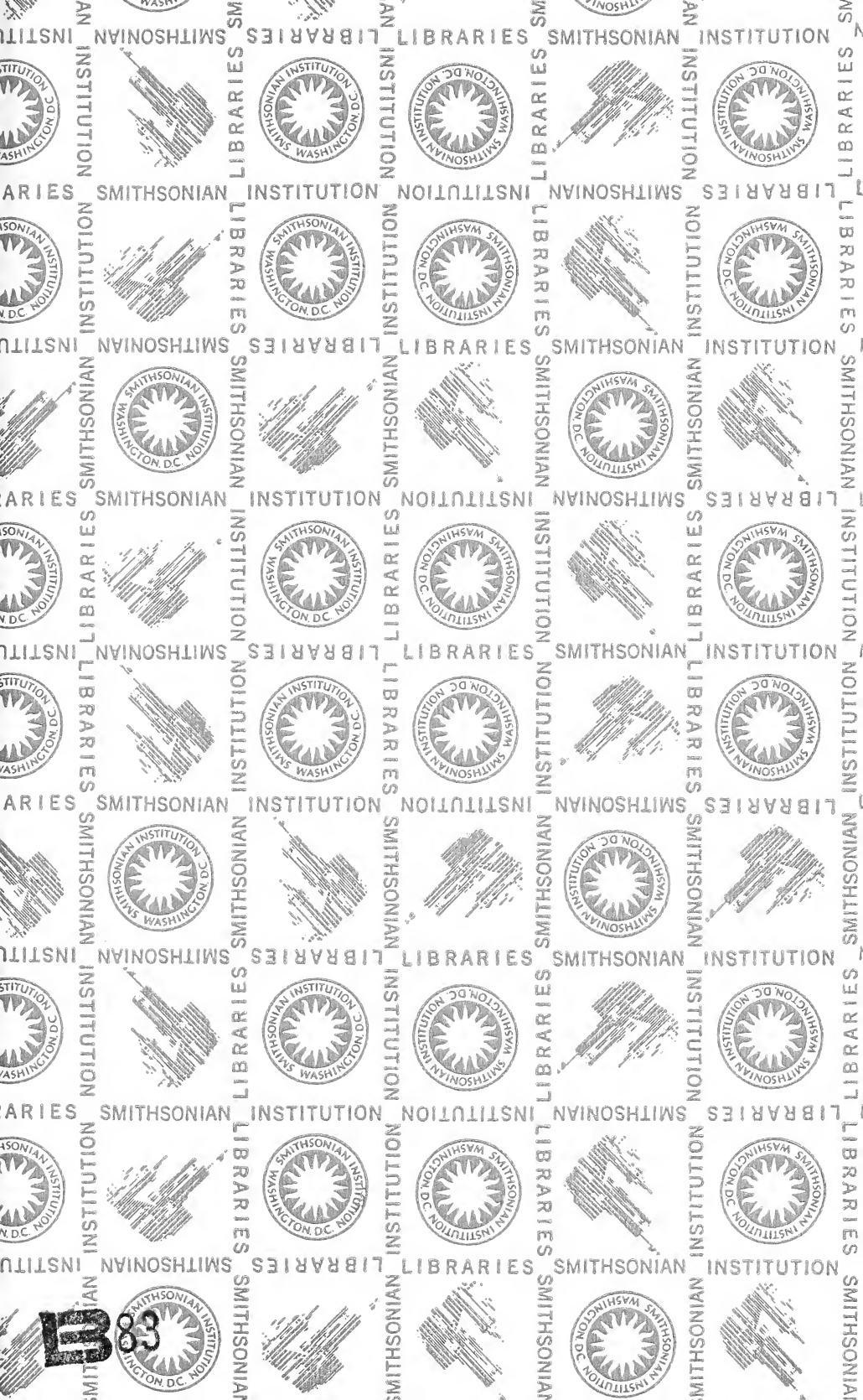
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